A special publication
compiled by the
Canadian Wildlife Service
for the
Pacific Seabird Group

Proceedings of the Pacific Seabird Group Symposium, Seattle, Washington, 6–8 January 1982

85-2315/

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Marine birds: their feeding ecology and commercial fisheries relationships

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Catalogue No. CW66-65/1984
ISBN 0-662-13311-0

Cover illustration by Barbara Dodge

This volume is dedicated to the memory of

Gordon A. Calderwood, research technician of the Seabird Research Unit, Canadian Wildlife Service, who drowned in Witless Bay, Newfoundland, on 6 July 1980 while conducting censuses of breeding seabirds,

Anne J. Vallée, wildlife biologist with the Canadian Wildlife Service and Ph.D. student in zoology at the University of British Columbia, who died on Triangle Island, British Columbia, on 31 July 1982 while performing studies on Tufted Puffins.

Gunnar Lid, research scientist with the Zoological Museum, Oslo, who drowned in seas off Røst, Norway, on 1 August 1983 while making observations on Atlantic Puffins at sea.

Preface

The papers in this volume were presented as a special symposium at the eighth annual meeting of the Pacific Seabird Group (PSG) held in Seattle, Washington, on 6–8 January 1982. The meeting and special symposium were co-sponsored by the Seattle Aquarium and Washington Department of Game. The program chairman for the meeting was Harry M. Ohlendorf. The hosts, the Washington Department of Game and the Seattle Aquarium, and the local committee chairmen, Lora L. Leschner and Gary Ballew, co-ordinated local arrangements.

The idea to hold a special symposium on the feeding ecology of seabirds originated at the executive council meeting in Tucson, Arizona, in November 1980. The council identified a series of integrated themes which together encompass a wide range of species groups and biological interests. First, they decided not to restrict the symposium to primary seabird species, rather to include marine waterfowl and their nearshore habitats. They wished to accomplish two goals: (1) to focus attention on the immense, undescribed flocks of waterfowl that play an important role in coastal marine ecosystems, particularly in the northeast Pacific where they are highly vulnerable to oil developments; and (2) to bring waterfowl and seabird investigators together to exchange technical information and conservation strategies. Once the executive council agreed to devote a full session to marine waterfowl and another to pelagic seabirds, discussion focused quickly on the need for a third session to review the effects of commercial fisheries on marine-associated birds. At that stage the special symposium was born, with session chairmen selected by the program chairman and endorsed by the executive council. The final task was for chairmen to identify and secure those individuals whose contributions might best meet the aims of the symposium and represent current thinking on their respective topics. Contributors were required to submit a draft of their paper to the editors prior to the symposium; after the meeting they could submit a revised draft before the official review was initiated. All papers were reviewed by at least two external referees (see "Reviewers of the special symposium") and the editors before they were accepted for the published proceedings. Papers listed under symposium sessions of the Pacific Seabirds Group eighth annual meeting *Program and Abstracts* guide which do not appear in this publication were withdrawn or rejected.

The symposium consisted of three parts: I. The feeding ecology of marine waterfowl (chairmen: P.F. Springer and J. King), II. The feeding ecology of pelagic marine birds (chairmen: G.A. Sanger and D.G. Ainley), and III. Seabird and commercial fisheries interactions (chairmen: D.N. Nettleship, G.L. Hunt, Jr., and A.D. MacCall). Session I comprises six papers which discuss aspects of the winter or summer feeding ecology of six waterfowl species inhabiting coastal waters of Alaska and British Columbia. The papers compare the usage of habitat types and food items, with some consideration of prey availability, trophic relationships, and resource partitioning. Session II contains seven papers, four of which present observations collected exclusively in the pelagic environment and three which deal with bird distribution and food data gathered at colonies during the breeding season or close to land. Three papers discuss various characteristics of the feeding ecology of the Sooty Shearwater at certain locations in the North Pacific. These reports, and other papers on chick diet and on oceanographic factors influencing the distribution and abundance of food in marine waters, illustrate the complexity of the feeding dynamics of seabird populations. Session III consists of 10 papers which attempt to show the interrelationships among species and the serious effects that commercial fisheries can have on seabird populations and communities by competing directly for food and by accidental drowning of birds in fish nets. Examples are drawn from regions throughout the world's oceans, wherever the appropriate studies have been conducted. Characteristics common to instances of competition between fisheries and seabird communities are highlighted. Also, the contributors underline differences in vulnerability between those systems where the target fish species forms the basis of the food web and those having a more diversified prey structure. They look at drowning of seabirds in fish gill nets in three different regions (from high arctic to boreal waters); and they show the wide variation in form that this source of mortality can take and how easily it can lead to a serious decline in a seabird population.

We hope that the 23 papers included in these proceedings will provide answers to some of the questions being posed by seabird and waterfowl workers concerning the feeding ecology of avian species inhabiting coastal and offshore marine habitats. They do at least bring together the findings of a number of individual investigations in their respective subject areas. We hope this volume will also provide the stimulus for much more research. For example, sessions I and II reveal the need for more detailed study of the diet of seabirds when they are away from land, particularly outside the breeding season, and for researchers to determine prey preference and consumption rates by comparing the use the birds make of habitats and food items to their availability. They also point to the need to study a

prey's availability relative to other potential prey. For understanding relationships between seabirds and other components of marine ecosystems, including fisheries, we must develop techniques that enable us to measure directly or estimate with known precision how much of a given prey seabirds eat per unit time. Only then will we be able to relate seabird diets to fisheries quantitatively and accurately. Information on these and other aspects of the feeding ecology of marine birds is required, not only to better understand the structure and function of avian components of marine ecosystems, but also to provide a bank of knowledge for evaluating the effects of both natural and man-induced environmental perturbations.

The symposium and these proceedings are the result of a tremendous amount of hard work on the parts of many people. The Washington Department of Game and the Seattle Aquarium, the co-sponsors of the meeting, together with Lora Leschner and Gary Ballew did an excellent job with the local arrangements. The Seattle Aquarium provided outstanding logistical support before and during the meeting, and free access to their fine marine exhibits. We owe special thanks to Harry Ohlendorf for the successful development and co-ordination of the scientific program including both the symposium and "contributed-paper" sessions, to Kees Vermeer for his support as chairman of the PSG executive council, and to David G. Ainley for his considerable contribution to the editing of symposium papers in session II. Joyce Dagnall has been of invaluable assistance, not only in dealing with the voluminous correspondence and retyping of manuscripts that took place through all phases of the symposium's development and completion, but also in organizing and maintaining the manuscript files for all sessions as revised drafts were received from authors and editors. Susan Johnson and Angela Nettleship have been extremely helpful with proof-reading certain parts of the galleys. We also are extremely grateful to Patricia Loshak, chief of Canadian Wildlife Service Scientific and Technical Publications Division, in guiding this volume through its various stages of development to publication, and to Susan Burns who performed the final edit and proof-reading of the entire manuscript. We are also grateful to the U.S. Fish and Wildlife Service for their support in permitting two of us (G.A.S. and P.F.S.) to participate and use office time to edit and prepare manuscripts, which in the end made possible the collaboration necessary to produce these proceedings.

Finally, we sincerely thank the authors for their contributions and the co-operative manner in which they collectively responded to suggestions for revision and editorial comments from external referees and the editors. We also extend our special thanks to those many individuals who served as reviewers of manuscripts (see section entitled "Reviewers of the special symposium"), whose combined efforts ensured that contributions accepted for publication attained a satisfactory scientific standard. In closing, we wish to express our gratitude to the Canadian Wildlife Service, Environment Canada, for providing the financial support and technical staff to publish these papers as a proceedings volume, and for allowing us to undertake the editing and preparation of the book at the Bedford Institute of Oceanography.

David N. Nettleship
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February 1984

Reviewers of the special symposium

The editors and authors thank the following individuals who served as referees of manuscripts submitted for publication in the symposium proceedings; it is only through their considerable efforts and care that we have succeeded in achieving a high scientific standard for papers presented in this volume (individuals who reviewed two or more manuscripts are indicated by an asterisk):

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Part I

Feeding ecology of marine waterfowl

Winter food habits of Barrow's Goldeneyes in southeast Alaska

by Philip S. Koehl[1], Thomas C. Rothe[2], and Dirk V. Derksen
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1. Abstract

Thirty-eight Barrow's Goldeneyes (*Bucephala islandica*) were collected in four neighbouring fiords of southeast Alaska in February 1980 and 1981. Esophageal and gizzard contents of the birds were examined separately to determine major prey species. Their diets consisted almost entirely of molluscs and crustaceans, with almost no insects or plants. The mean volumetric percentages of the most common foods in combined esophagi and gizzards were as follows: blue mussel (*Mytilus edulis*), 53.1; discord mussel (*Musculus discors*), 11.1; barnacle (*Balanus glandula*), 12.0; puppet margarite snail (*Margarites pupillus*), 8.3; hermit crab (*Pagurus hirsutiusculus*), 6.2; Sitka periwinkle (*Littorina sitkana*), 1.3; and algae, <0.1.

No difference in diet composition by sex was detected, but males selected larger blue mussels than did females. The number of food taxa consumed in 1981 ranged from 5 to 28 among fiords, and 1 to 18 among individual birds. The number of food taxa in birds from one fiord was 30 in 1980, and only 12 in 1981. This study suggests that goldeneyes feed within 2 m of the surface on a variety of foods depending upon tide height, but blue mussels are selected at depths through 4 m.

2. Résumé

En février 1980 et 1981, 38 Garrots de Barrow (*Bucephala islandica*) ont été recueillis dans quatre fiords voisins du sud-est de l'Alaska. Nous avons examiné séparément le contenu de l'œsophage et du gésier des oiseaux pour déterminer les principales espèces constituant leurs proies. Leur régime se composait presque entièrement de mollusques et de crustacés et ne comportait pratiquement pas d'insectes ni de plantes. Les pourcentages volumétriques moyens des aliments les plus fréquents dans les œsophages et gésiers combinés étaient : la moule bleue (*Mytilus edulis*), 53,1; la moule lisse (*Musculus discors*) 11,1; la balane (*Balanus glandula*) 12,0; la margarite pupille (*Margarites pupillus*), 8,3; le bernard-l'hermite (*Pagurus hirsutiusculus*), 6,2; la littorine sitka (*Littorina sitkana*), 1,3; et les algues, <0,1.

Nous n'avons pas trouvé de différences entre les régimes des deux sexes, mais les mâles prenaient des moules bleues plus grosses que ne le faisaient les femelles. Le nombre de taxons alimentaires consommés en 1981 variait de 5 à 28 selon les fiords et de 1 à 18 selon les oiseaux considérés individuellement. Le nombre de taxons alimentaires consommés par les oiseaux d'un fiord s'élevait à 30 en 1980, mais tombait à 12 en 1981. D'après cette étude, les garrots se nourriraient jusqu'à une profondeur de 2 m de toute une variété d'aliments, tout dépendant de la hauteur de la marée, mais iraient pêcher les moules bleues jusqu'à 4 m de profondeur.

3. Introduction

In 1980, personnel of the United States Fish and Wildlife Service (USFWS) initiated baseline studies of heavy-metal concentrations in marine birds and their prey to detect impacts of tailings disposal at the proposed Quartz Hill molybdenum mine in southeast Alaska. The areas of study, about 60 km east of Ketchikan in Misty Fjords National Monument, are characterized by long, granite-walled inlets with steep, rocky shores and a maximum tidal range of 7 m. A part of these studies is the analysis of food habits of the Barrow's Goldeneye (*Bucephala islandica*), the area's most abundant wintering seaduck. The diet of this species was first discussed by Munro (1918) and Yorke (1899, cited in Bent 1925). More complete descriptions of their food habits, including birds from British Columbia, were given by Munro (1939), Cottam (1939), and Vermeer (1982).

This study was designed to examine the major foods of wintering Barrow's Goldeneyes and to explore the effects that food availability may have on diet composition and foraging patterns.

4. Methods

All birds were taken with a shotgun from a skiff. Because they were wary, birds were seldom observed feeding. After collection, birds were labelled and taken to a research vessel where they were weighed, sexed by internal examination, and emptied of stomach contents.

Because this work was ancillary to the investigation of heavy metals in seaducks, some procedures recommended for food habits studies (Swanson and Bartonek 1970) were not followed. In 1981, esophageal and gizzard contents were removed, weighed, sealed in jars and frozen 1–3 h after collection. Samples were thawed, preserved in 10% Formalin, and examined 6 weeks later. The gut contents of birds collected in 1980 were preserved in 10% Formalin and examined 13 months later.

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Preserved food items were sorted to taxon, identified to species when possible, then air-dried and weighed, measured volumetrically by liquid displacement, and counted. We estimated the percentage composition of food items in four birds because the gizzard contents could be identified but were inseparable. Frequency of occurrence, mean of volumetric percentages, and percentage of total volume were calculated for each prey species (Swanson *et al.* 1974).

We used two-way analysis of variance tests on arc sine transformed percentage data to compare diets of male and female ducks, and one-way analysis of variance tests on $\ln$ transformed count data to test for differences in diet by tide stage. We used t-tests to compare sizes of invertebrates (Sokal and Rohlf 1969); sizes are expressed as $\bar{x} \pm$ SE. Vertical distributions of intertidal prey species were observed in the field and verified in the literature (Ricketts and Calvin 1968, Abbott 1974) and by Richard T. Myren, National Marine Fisheries Service, Juneau (pers. comm.).

References used for identifying prey are Abbott (1974), Barnard (1969), Butler (1980), Foster (1981), Keen and Coan (1974), Kozloff (1974), McLaughlin (1974), Oldroyd (1925–27), Pennak (1978), Pilsbry (1916), Smith and Carlton (1975), and Wiggins (1978).

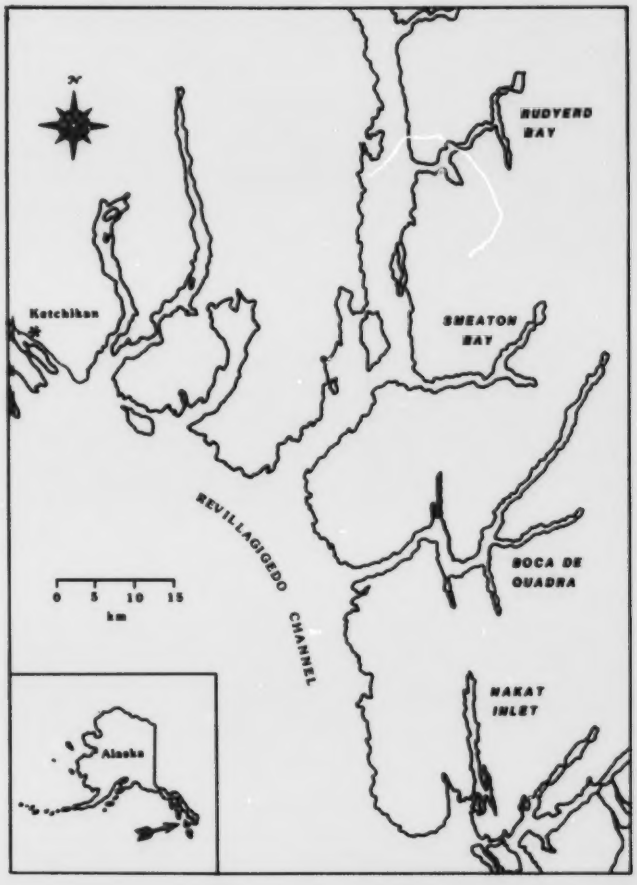
5. Results

Thirty-eight Barrow's Goldeneyes were collected in Misty Fjords National Monument: 10 from Boca de Quadra in February 1980, and 7 each from Boca de Quadra, Nakat Inlet, Smeaton Bay, and Rudyerd Bay (Fig. 1) in February 1981. Of 43 food taxa identified, five comprised over 90% of the combined mean volumetric percentage (Table 1). They were the blue mussel (*Mytilus edulis*), the discord mussel (*Musculus discors*), the puppet margarite snail (*Margarites pupillus*), a barnacle (*Balanus glandula*), and a hermit crab (*Pagurus hirsutiusculus*). Animals smaller than 10 mm were probably ingested incidentally with larger prey species. For example, the molluscs *Granulina margaritula*, *Spiroglyphus lituellus*, and *Hiatella arctica* were only found entangled in the byssal "cocoons" of discord mussels, and very small blue mussels were found clustered with larger mussels. Encrusting ectoprocts (bryozoans) were associated exclusively with gastropods. Although half of the stomachs contained algae, their mean volumetric percentage was less than 0.1. Algal fragments were usually attached to or entangled with byssal threads of mussels.

Only nine birds had esophageal contents. Two-way analysis of variance was used to test for differences in the volumetric percentages of five major food taxa between esophagi and gizzards. No significant difference ($P>0.05$) in proportions of foods was found, so data were combined for each of these birds.

The diets of 23 male and 15 female Barrow's Goldeneyes were compared, but no significant differences in the mean volumetric percentages of five major food taxa were found ($P>0.05$). However, significantly larger blue mussels ($t=4.83$, $P<0.05$) were eaten by males ($\bar{x}=16.6 \pm 1.3$ mm, $n=36$) than by females ($\bar{x}=9.9 \pm 0.4$ mm, $n=145$), although no significant differences in sizes of other prey could be detected. Ingested blue mussels, the largest prey eaten, ranged from 2.3 to 37.0 mm ($\bar{x}=11.3 \pm 0.5$, $n=181$) in length. Other prey sizes ranged from 2.2 to 22.2 mm ($\bar{x}=10.6 \pm 0.6$, $n=62$) for discord mussels, up to 12.4 mm for barnacles, and to 23.3 mm for shells (*Nucella lamellosa*) used by hermit crabs.

Figure 1
Four fiords in southeast Alaska where Barrow's Goldeneyes were collected, February 1980 and 1981



Numerous bays and several river deltas provide diverse sand and cobble habitats for prey species in Boca de Quadra. Birds collected in that fiord ate a total of 32 taxa in both years of our study, and they ate 13 taxa that were not found in birds from the other fiords. We suspect that a decline in food variety from 30 taxa in 1980 to 12 in 1981 is an artifact of collecting birds at different tide stages between years. Birds from Rudyerd Bay contained only five taxa, and those from Smeaton Bay contained eight. Both Rudyerd and Smeaton Bays have near vertical walls and little diversity of intertidal habitats; several birds from these fiords had fed exclusively on blue mussels. Nakat Inlet, with more gently sloping shores, has more extensive intertidal sand and gravel beaches. Nakat goldeneyes consumed 28 taxa, including six foods not found in the other fiords; a single bird from Nakat Inlet contained 18 prey species. Prey availability may differ among fiords; however, over half the birds from Nakat Inlet were collected at low tides, whereas all but one of the Rudyerd Bay birds were collected at high tides.

Thirty-one goldeneyes in this study and at Port Valdez in southcentral Alaska (Derksen, unpubl. data), contained whole or undigested organisms. By relating the tide stage at the time of collection to the vertical distribution of prey species in the intertidal zone, we estimated the depths to which goldeneyes dove to feed. We used this

Table 1
Volumes and frequencies of food items from Barrow's Goldeneyes in southeast Alaska, February 1980 and 1981

Taxon	Esophageal contents ($N = 9$)			Gizzard contents ($N = 37$)			Combined contents ($N = 38$)		
	Mean vol., %	% total vol.	% occur.	Mean vol., %	% total vol.	% occur.	Mean vol., %	% total vol.	% occur.
Algae	tr*	tr	56	tr	tr	46	tr	tr	50
Mollusca									
Polyplacophora									
Tonicella insignis	—	—	—	tr	0.1	8	tr	tr	8
Tonicella lineata	0.1	0.1	33	tr	0.1	19	0.1	0.1	18
Mopalia lignosa (?)	—	—	—	tr	0.1	3	tr	tr	3
Gastropoda									
Acmaea mitra	—	—	—	0.1	0.1	3	0.1	0.1	3
Collisella spp.	—	—	—	tr	tr	16	tr	tr	16
Cryptobranchia alba	tr	0.1	33	tr	tr	8	tr	tr	8
Calliostoma ligatum	—	—	—	0.1	tr	5	0.1	tr	5
Lirularia lirulatus	—	—	—	tr	tr	3	tr	tr	3
Margarites helicinus	0.2	0.1	22	tr	tr	5	tr	tr	8
Margarites pupillus	1.2	2.0	22	9.1	9.0	30	8.3	7.6	29
Lacuna spp.	0.1	tr	44	tr	tr	22	tr	tr	24
Littorina scutulata	tr	tr	11	0.3	0.4	14	0.3	0.3	13
Littorina sitkana	tr	tr	22	1.4	1.2	24	1.3	1.0	32
Alvinia compacta	—	—	—	tr	tr	5	tr	tr	5
Spiroglyphus lituellus (?)	tr	tr	33	tr	tr	16	tr	tr	16
Bittium sp.	—	—	11	0.7	0.9	14	0.7	0.8	13
Melanella sp.	—	—	—	tr	tr	3	tr	tr	3
Natica clausa	—	—	—	1.8	2.0	5	1.7	1.6	5
Ocenebra interfossa	—	—	—	0.3	0.2	16	0.3	0.1	16
Urosalpinx lurida	—	—	—	tr	tr	8	tr	tr	8
Amphissa columbiana	tr	tr	11	0.8	1.2	8	0.8	1.0	11
Nassarius mendicus	—	—	—	0.3	0.4	5	0.3	0.3	5
Oenopota sp.	—	—	—	tr	tr	8	tr	tr	8
Granulina margaritula	tr	tr	11	tr	tr	8	tr	tr	11
Odostomia sp.	—	—	—	tr	tr	5	tr	tr	5
Unidentified spp.	—	—	—	0.2	0.2	11	0.2	0.1	11
Bivalvia									
Musculus discors	29.9	46.3	44	10.9	18.1	24	11.1	21.9	24
Mytilus edulis	66.6	49.2	89	54.5	39.9	87	53.1	40.1	84
Saxidomus gigantea	—	—	—	1.7	2.5	5	1.7	2.1	5
Hiatella arctica	tr	0.1	33	tr	tr	11	tr	tr	11
Crustacea									
Balanus glandula	tr	tr	78	12.5	15.0	78	12.0	12.2	84
Gnorimosphaeroma oregonensis	tr	tr	22	tr	tr	3	tr	tr	5
Amphipoda (Gammaridae)	—	—	—	tr	tr	8	tr	tr	8
Pandalus tridens	—	—	—	—	—	—	0.2	0.3	3
Heptacarpus sp.	—	—	—	—	—	—	0.2	0.3	3
Hemigrapsus nudus	—	—	—	0.3	0.6	14	0.7	1.0	16
Pagurus hirsutiusculus	—	—	—	4.6	8.0	14	6.2	8.7	16
Unidentified spp.	tr	tr	11	tr	tr	14	tr	tr	13
Insecta									
Trichoptera (larva)									
Limnephilus sp.	—	—	—	tr	tr	3	tr	tr	3
Diptera (pupa)	—	—	—	tr	tr	3	tr	tr	3
Ectoprocta									
Hippothoa hyalina	tr	tr	22	—	—	—	tr	tr	5
Echinodermata									
Asteroidea	1.8	2.0	11	tr	tr	3	0.1	0.3	3
Strongylocentrotus droebachiensis	0.1	0.1	22	tr	tr	11	tr	tr	13

*tr = values less than 0.05.

information to identify some general prey-use patterns. We defined the mid-intertidal zone as 1.0–3.2 m above Mean Lower Low Water, which is approximately the middle third of the extreme, local tide range (−1.4 to 5.8 m). The plant and animal communities we observed in the upper, middle, and lower intertidal zones typify those described by Ricketts and Calvin (1968) for rocky shores of bays and estuaries in the northern Pacific. The intertidal zonation is similar to that of Port Valdez (Myren, pers. comm.), and depths at which molluscs are found have been described by Abbott (1974) for nearby geographic locations.

Goldeneyes feeding during low tides both in our study area and at Port Valdez ate a significantly greater variety of prey ($F = 10.78$, $P < 0.01$) than did those feeding at higher tide stages (Table 2). Twenty-three species, including 13 gastropods, 2 chitons, a bivalve, and 5 polychaete annelids were eaten by goldeneyes only when the tides were low. The purple shore crab (*Hemigrapsus nudus*), the yellow-legged shrimp (*Pandalus tridens*), and two freshwater insect taxa were taken solely during high tides. Gut contents of birds collected on high and mid tides (above 1.0 m) consisted predominantly of blue mussels with attached barna-

Table 2
Mean number of prey taxa consumed by Barrow's Goldeneyes at different tide stages

Fiord	High tide above 3.2 m $\bar{x} \pm$ se (*N*)	Mid tide 1.0–3.2 m $\bar{x} \pm$ se (*N*)	Low tide below 1.0 m $\bar{x} \pm$ se (*N*)
Nakat Inlet	6.0 ± 0.0 (3)	—	9.8 ± 3.1 (4)
Boca de Quadra	3.7 ± 1.3 (3)	4.8 ± 1.1 (4)	—
Smeaton Bay	2.0 ± 0.3 (5)	—	5.5 ± 2.5 (2)
Rudyerd Bay	2.3 ± 0.3 (6)	4.0 (1)	—
Port Valdez*	2.6 ± 0.5 (5)	2.0 (1)	11.0 ± 4.0 (2)
All areas	3.0 ± 0.4 (22)	4.2 ± 0.8 (6)	9.0 ± 1.9 (8)

*From a separate study (Derksen, unpubl. data).

cles and periwinkles, and rarely of prey normally found at lower elevations. Goldeneyes collected at low-water stages (below 1.0 m), when blue mussels were exposed and unavailable, had eaten lower intertidal and sub-tidal prey, such as the discord mussel; the gastropods *Margarites pupillus*, *Bittium* sp., *Calliostoma ligatum*, *Natica clausa*, *Amphissa columbiana*; and the urchin *Strongylocentrotus droebachiensis*.

Except for blue mussels, all undigested prey species found in these goldeneyes and those collected throughout the winter near Valdez are known to inhabit intertidal and sub-tidal areas that were within 2 m of the water's surface at the time we collected the birds. Undigested blue mussels, however, the most commonly eaten food, were found in birds that we collected when water levels were more than 4 m above mussel beds.

6. Discussion

The bias associated with using gizzard contents to assess the relative importance of different foods in waterfowl diets is primarily due to differential digestion of plant and animal tissues (Bartonek and Hickey 1969, Swanson and Bartonek 1970). This bias is probably minimal in our results for wintering goldeneyes because (1) plant foods comprised a very small part of diets; (2) calcareous-shelled animals and animals with calcified, chitinous exoskeletons comprised over 95% by volume of esophageal and gizzard contents; (3) except for the ectoproct, *Hippothoa hyalina*, whose volume was not measurable, no prey were found in esophagi that were not also found in gizzards; and (4) for nine goldeneyes with esophageal contents, there were no significant differences in relative food volumes between esophagi and gizzards.

The gut contents of each bird collected represent a small temporal sample of its complete diet. Swanson and Bartonek (1970) found in Blue-winged Teal (*Anas discors*) that all amphipods, 82% of snails (*Gyraulus* spp.), and 24% of diptera larvae were not identifiable 10 min after ingestion. Grandy (1972) demonstrated that Black Ducks (*Anas rubripes*) can pass blue mussels through their digestive tracts in 30–45 min. Mallards (*Anas platyrhynchos*) can excrete crayfish (*Cambarus* spp.) within 45 min of ingestion (Malone 1963). Because of rapid digestion rates, we assumed that nearly whole or undigested animals found in either the esophagus or gizzard were recently eaten, and could therefore be related to the tide stage at the time of collection.

Munro (1939) and Vermeer (1982) found that blue mussels were the main diet of Barrow's Goldeneyes wintering in British Columbia marine habitats. Cottam (1939) did not present his data by season, but stated that mussels and, moreover, insects were important foods. Vermeer's (1982) study more clearly demonstrates seasonal differences in goldeneye diets. He found that they feed mostly on herring eggs during their northward migration in spring.

The diet and feeding ecology of the Common Goldeneye (*Bucephala clangula*) are better known and present some opportunities for a comparison of feeding strategies. In British Columbia, where winter ranges of goldeneyes overlap, Common Goldeneyes seem to rely more on crustaceans and less on mussels than do Barrow's Goldeneyes (Munro 1939, Vermeer and Levings 1977, Vermeer 1982). A single Common Goldeneye that we collected from Smeaton Bay contained amphipods (*Anisogammarus confervicolus*), isopods (*Gnorimosphaeroma oregonensis*, *Idotea wosnesenskii*), hermit crabs (*Pagurus hirsutiusculus*), trichopteran larvae (*Limnephilus* sp.), pieces of plant material, fish probably Pacific sandlance (*Ammodytes hexapterus*), and a limpet (*Notoacmea fenestrata*). Common Goldeneyes in Denmark (Madsen 1954) and Great Britain (Olney and Mills 1963) also ate mostly crustaceans, but those wintering off the coast of Sweden fed predominantly on mussels and secondarily on crustaceans (Nilsson 1972), similar to the Barrow's Goldeneyes in our study.

Nilsson (1970) demonstrated that Common Goldeneyes feed with great intensity during winter, and only during daylight hours. He concluded that thermal stress and limited daylight in winter could put goldeneyes in a marginal position in meeting their nutritional requirements. If we infer the same limitations for Barrow's Goldeneyes, selection pressure would seem to greatly encourage optimization of food selection and foraging effort.

We have presented evidence that Barrow's Goldeneyes select foods differentially at various tide stages. The influence of tides in feeding has also been observed in Common Scoters (*Melanitta nigra*) (Mudge and Allen 1980), Common Eiders (*Somateria mollissima*) (Player 1971, Cantin *et al.* 1974, Campbell 1978), and Black Ducks (Grandy and Hagar 1971). We suggest that Barrow's Goldeneyes minimize their diving efforts by shifting to different prey species with tide changes. The food value gained per unit of foraging effort for blue mussels may be sufficiently high to benefit goldeneyes diving deeper than 2 m. Such an opportunistic feeding strategy would be advantageous during periods of high energy expenditures.

Aerial surveys by Conant and King (1981) indicate that as many as 30 000 goldeneyes winter in the northern half of southeast Alaska. More information on the behaviour and habitats of these birds is needed to assure their protection from shoreline modifications, oil spills, and mine-waste pollution. Blue mussels, a favoured prey, are well known for their ability to concentrate pollutants at high levels (Goldberg 1975). Mining and petroleum activities are expected to increase dramatically in southeast Alaska, challenging all of us to see that coastal resources are considered in the process.

7. Acknowledgements

We thank William Eldridge, J. Chris Franson, and Robin West who participated in data collection, Nora Foster of the University of Alaska Museum for valuable taxonomic assistance, Richard T. Myren of the Auke Bay Fisheries Laboratory for information on intertidal communities, and Debbie Amos and SuzAnne Miller for statistical advice. The M/V Curlew and skipper, Ted Estrada, were provided by the USFWS, Southeast Alaska Ecological Services, Juneau.

We are grateful to Anthony J. Erskine, Lori Hawkins, Mary Hogan, Margaret Petersen, Gerald A. Sanger, and Paul F. Springer for reviewing the manuscript and providing helpful comments.

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Coastal feeding ecology of Harlequin Ducks in Prince William Sound, Alaska, during summer

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1. Abstract

Feeding habitat and time allocated to feeding changed from early to late summer among Harlequin Ducks (*Histrionicus histrionicus*) studied in Prince William Sound, Alaska, during summers 1979 and 1980. In early summer, harlequins fed predominantly in the intertidal deltas of small streams, and in the intertidal zones of protected bays, where they consumed a variety of marine invertebrates. Following the arrival of spawning salmon in July, harlequins moved into the lower portions of suitable streams and fed on drifting roe. In May and early June, before incubation began, paired female and male harlequins spent, respectively, about 21 and 13% of their diurnal time (04:00–23:00) feeding (ingesting prey, diving, and dabbling). Following dissolution of pairs in mid June, single females and males spent, respectively, 15 and 12% of their diurnal time (05:00–22:00) feeding.

2. Résumé

Parmi les Canards arlequins (*Histrionicus histrionicus*) étudiés dans le détroit de Prince-William (Alaska) durant les étés de 1979 et de 1980, l'habitat d'alimentation et le temps consacré à l'alimentation changeaient entre le début et la fin de l'été. Ainsi, au début de l'été, les canards se nourrissaient surtout dans les deltas intertidaux des petits cours d'eau et dans les zones intertidales des baies protégées où ils consommaient toute une variété d'invertébrés marins. En juillet, après l'arrivée des saumons en période de frai, les canards se déplacaient vers les parties inférieures des cours d'eau appropriés pour se nourrir des oeufs à la dérive. En mai et au commencement de juin, avant le début de l'incubation, les femelles et les mâles appariés passaient respectivement 21 % et 13 % environ de leur temps diurne (de 4:00 à 23:00) à se nourrir (c'est-à-dire à ingérer leurs proies, à plonger et à barboter). Après la dissolution des couples à la mi-juin, les femelles et les mâles séparés consacraient respectivement 15 % et 12 % de leur temps diurne (de 5:00 à 22:00) à se nourrir.

3. Introduction

The feeding ecology of the Harlequin Duck (*Histrionicus histrionicus*) in North America is poorly known. Along the coast in winter, harlequins apparently feed on a wide variety of foods, but predominantly on crustaceans (mostly crabs and amphipods) and mollusks (especially chitons and gastropods) obtained in shallow and often turbulent water near shore (Bent 1925, Cottam 1939, Kenyon 1961, Palmer 1949, Preble and McAtee 1923, Whitfield 1894). During the summer, along streams located relatively far inland, breeding harlequins feed on blackfly (Simuliidae) larvae, and on aquatic Trichoptera, Chironomidae, and Perlidae (Bengtson 1972, Dement'ev and Gladkov 1952, Gudmundsson 1971). In Iceland during summer, harlequins along inland streams feed in shallow (<80 cm) rapids near suitable nesting and loafing sites, or they may fly upstream to feed near the outlets of lakes (Bengtson 1972:13). Harlequins use both running and standing water in Montana during summer, and backwater ponds are important there for feeding during high-water periods and during brood rearing (Kuchel 1977:93).

In spring (about April) harlequins migrate from exposed coasts into fiords and bays where they congregate near river mouths before moving inland (Bengtson 1966, Gudmundsson 1971). However, not all harlequins travel far inland; many breed along streams close to the coast (Gabrielson and Lincoln 1959, Palmer 1976, Dzinbal 1982). In addition, most non-breeders remain on the coast during the summer, where they are eventually joined by post-breeding drakes and failed-breeding females (Palmer 1976).

However, little information exists concerning the feeding activity of harlequins or the particular sites they prefer to forage in along the North American coasts during summer. This study was conducted to compare the diurnal feeding activity of harlequins to their habitat use in a small bay in Prince William Sound, Alaska, during the summers of 1979 and 1980. A second objective was to obtain information on their food.

4. Study area

Sawmill Bay, the primary study area, lies in northeast Prince William Sound about 24 km southwest of Valdez, Alaska (Fig. 1). The study area lies within the Coastal Spruce–Hemlock Forest vegetation region (Viereck and Little 1972). The area has a moderate climate characterized by cool, rainy summers and winters with heavy snowfall. Ice fields and glaciers are prominent at higher elevations in the surrounding mountains. The geography, climate, glacial history, and vegetation of Prince William Sound are discussed by Cooper (1942).

Sawmill Bay has a water area of 2.25 km^2 (Fig. 1), is about 18 m deep at its mouth, and is enclosed by steep mountains rising 1000–1370 m. Tides fluctuate 2–6 m in the bay, and at low tide a large portion of the bay lies exposed. Three short (about 5 km) streams with discharge

rates of about 1.5–7.0 m^3/s enter the bay (Dzinbal 1982). Only Stellar Creek, a moderately steep, clear, non-glacial stream, received appreciable use by harlequins, mostly below the confluence of Fault Creek (Fig. 1). Only incubating and brooding females regularly occurred farther upstream.

About 50 harlequins (including 14–15 pairs) were present in Sawmill Bay at the peak of the breeding season in late May each year. In 1979 and 1980, respectively, 11 and 8 of the pairs observed in late May were thought to have attempted nesting along Stellar Creek (Dzinbal 1982). The other 3–7 pairs either nested on streams outside of the Sawmill Bay drainage or failed to nest.

5. Methods

Three habitats used by Harlequin Ducks in Sawmill Bay were distinguished: creek (Stellar Creek including the intertidal delta), rocks (offshore rocks, headlands, and small islands, including their immediately adjacent waters), and lee waters (quiet coves or areas in the lee of islands or peninsulas that were sheltered from all but the most violent storms).

Occurrence and feeding activity in the three habitats were assessed (1) for paired male and female harlequins during the pre-nesting and laying period (10 May – 21 June), and (2) for single males and females during the post-laying period (22 June – 15 August). Single males included both successful and unsuccessful breeders; single females were mostly failed or non-breeders (Dzinbal 1982). Data were not gathered for incubating or brooding females, which were secretive and difficult to monitor.

Harlequins appear to be daytime feeders only (Johnsgard 1975:411, Dzinbal 1982), and diurnal hours of study extended from 04:00–23:00 (Alaska DT) during the pre-nesting–laying period, and from 05:00–22:00 during the post-laying period.

Forty-three censuses were conducted during the pre-nesting–laying period and 37 during the post-laying period. Censuses lasted about 1 h each, and were conducted from an inflatable boat travelling at 8–20 km/h, 10–20 m off shore; stops were made on shore at selected vantage points to ensure maximum visual coverage of the study area. Visibility of harlequins in Sawmill Bay was good, and censuses were assumed to record virtually all harlequins present. Observations were conducted from a distance with 10X binoculars to minimize disturbance, and each group was observed long enough to insure all individuals were counted. The proportion of time harlequins occurred in each habitat was estimated from pooled morning, midday, and evening censuses of the study area. Results were similar each year and, consequently, data from both years were combined. Chi-square goodness-of-fit tests among treatments (habitats) were conducted on census totals.

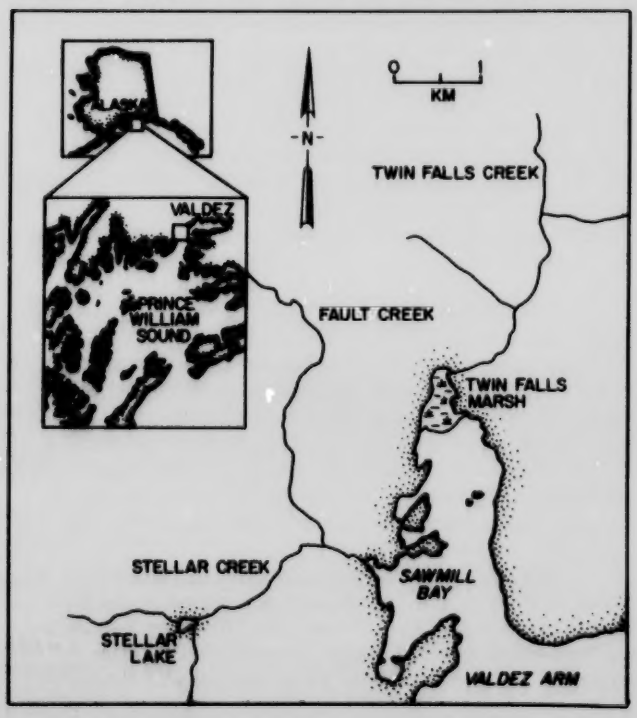
Diurnal feeding activity was determined in each habitat by recording, every 60 s, the behaviour of both the male and the female of randomly selected pairs, or of randomly selected single individuals. Censuses and observations of activities were conducted at separate times. Only those pairs or individuals watched continually for at least 10 min were included in analyses. Observations were obtained throughout all daylight hours but were pooled for analyses. Feeding behaviour, as used here, included only the actual time spent under water when diving, or time actually engaged in ingesting food, dabbling, or tipping-up. Time spent in locomotion, "peering" (i.e. inserting the bill and eyes vertically into the water), or other behaviour between feeding acts was not considered feeding behaviour. Comparisons of feeding rates (sex *vs* habitat and season) were made with chi-square tests of independence using a tabular χ^2 value corrected for multiple comparisons (cf. Neu *et al.* 1974).

Aggregate density of pink salmon (*Onchorhynchus gorbuscha*), chum salmon (*O. keta*), and anadromous Dolly Varden (*Salvelinus malma*) was indexed once every 7–10 days from 1 July – 20 August 1980 at five stations in lower Stellar Creek, below Fault Creek, by counting the number of stationary individuals present in a 1-m wide transect across the creek.

Drift samples of 2-h duration were continuously collected for a 24-h period, at 1–2-week intervals, to measure the rate of export of loose, drifting roe and invertebrates. Samples were collected from 3 June – 13 August 1980 at each of two stations in Stellar Creek (below Fault Creek). Each drift sampler consisted of a bag of aquatic netting (40 meshes per cm, 50 cm deep) supported inside an aluminum frame to maintain a square mouth of 25 × 25 cm. Samplers were placed at the foot of shallow riffles and, except occasionally during storm spates, they sampled the entire vertical water column. Salmon eggs and invertebrates were sorted from preserved samples and dried to constant weight at 45°C. Major invertebrate taxa collected in samples included Chloroperlidae, Baetidae, Heptageniidae, and Oligochaeta. However, neither the selectivity of the harlequins nor that of the drift samplers for specific invertebrates was known. Consequently, invertebrates in the drift samples were, for quantitative purposes, treated as a single, unified group and were not sorted taxonomically.

Five harlequins (two from Sawmill Bay and three from similar areas in Valdez Arm) were collected for food

Figure 1
Sawmill Bay study area, northeast Prince William Sound, Alaska



analyses after they had been observed feeding for a minimum of 10 min. Upon collection, 70% ethanol was injected into the esophagus, and the esophagus, proventriculus, and gizzard were removed and stored in 70% ethanol. Esophageal contents were analysed separately from those of the proventriculus and gizzard.

6. Results

Harlequin Ducks feeding at Stellar Creek remained almost exclusively in the intertidal zone outside the mouth of the creek until the first week of July (Fig. 2*A*). They fed most actively in the morning at all tide stages (Dzinbal 1982), but feeding was most intense when ebb and low tides occurred in the morning, a pattern similar to feeding activity of Common Eiders (*Somateria mollissima*) in Scotland (Campbell 1978). Harlequins feeding outside Stellar Creek most often dabbled or tipped-up at the edge of tidewater. They usually gleaned algae or probed in and sifted substrate sediments. Harlequins seemed to be opportunistic feeders, and were observed ingesting small crabs, snails, and worms while foraging in the delta of Stellar Creek. Stomachs of five harlequins contained mostly crabs (Decapoda), *Littorina* snails, and, in one case, starfish (Asteroidea) (Table 1).

After the first week of July, harlequins began feeding in the lower 1 km of Stellar Creek, and essentially ceased feeding in the intertidal area outside the mouth of the creek (Fig. 2*A*). The shift in feeding areas by harlequins coincided with a marked increase in both the abundance of salmon in the stream (Fig. 2*B*) and in the rate of drift of invertebrates and salmon eggs (Fig. 2*C*). Salmon eggs were abundant in stream drift samples from late July through early August, primarily because of the disruption of stream gravels and established salmon beds by late-arriving salmon and by storm freshets. The same processes probably caused the increased drift of invertebrates. Biomass of salmon eggs in late July and August was about one-third to one-half again as great as the biomass of invertebrates, but the difference was not significant ($t = 0.58$; $P>0.10$). However, relatively few salmon eggs comprised the total egg biomass ($\bar{x} = 15.7$ eggs/sample h from 31 July – 13 August), whereas several hundred or more individual invertebrates were captured per hour in the same samples. Harlequins, as well as hundreds of Glaucous-winged Gulls (*Larus glaucescens*), were observed feeding upon these waste eggs as they drifted downstream or where they collected in eddies or lodged behind debris obstacles.

The amount of time harlequins spent in each habitat varied. Harlequin pairs during pre-nesting and laying spent more time around rocks than at Stellar Creek or in lee waters ($\chi^2 = 28.2$, 2 df; $P<0.005$) (Table 2). Single males during the post-laying period spent more time around rocks than at Stellar Creek ($\chi^2 = 38.2$, 1 df; $P<0.005$), but single females divided their time equally between Stellar Creek and rocks ($\chi^2 = 3.8$, 1 df; $P>0.05$) (Table 2).

Despite their predominant occurrence around rocks, harlequins fed most actively at Stellar Creek, and least actively at rocks (Table 3). Paired females at Stellar Creek fed more actively during pre-nesting–laying (43%) than did single females there during the post-laying period

Figure 2
(*A*) Mean maximum daily count of Harlequin Ducks in the intertidal delta of Stellar Creek (intertidal) and in the non-tidal, lower portion of Stellar Creek proper (Stellar Creek) from May to September 1980; (*B*) Mean and 95% confidence intervals of the index to salmonid (*Onchorhyncus* spp. and *Salvelinus malma*) abundance in lower Stellar Creek during 1980; (*C*) Dry weight biomass (mean and 95% confidence intervals) of invertebrates and salmon eggs collected (per hour) in drift samples from lower Stellar Creek during 1980

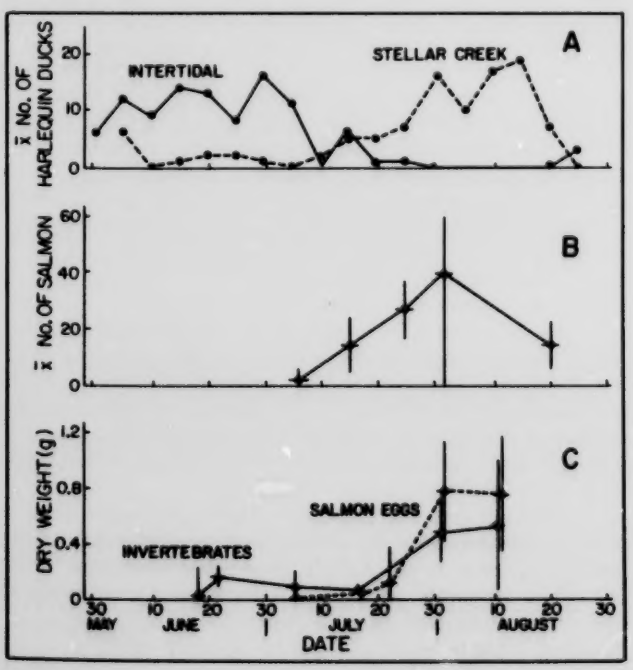


Table 1
Esophageal and stomach contents of two Harlequin Ducks collected from Sawmill Bay (specimens 1 and 2)* and three from Valdez Arm (specimens 3–5)†, summer 1980. Values are percent of total food volume (wet)

	Esophagus			Proventriculus and gizzard				
Specimen number	**1**	**2**	**3**	**1**	**2**	**3**	**4**	**5**
Total food volume, mL	**7.9**	**0.5**	**0.1**	**0.6**	**1.5**	**3.7**	**2.1**	**1.2**
Echinodermata								
Asteroidea (*Leptasterias*?)	95.7							
Insecta								
Diptera			30.0	4.9				
Crustacea								
Isopoda								1.7
Decapoda								
Brachyura (Brachyrhyncha)		2.8	19.4					
Anmomura (Paguroidea)					53.1	71.4	25.0	17.2
Unidentified Decapoda		33.3	60.0					
Mollusca								
Macoma balthica		1.1						
Macoma calcarea		3.3						0.9
Unidentified *Macoma*	0.3							
Mytilus edulis	0.8						26.9	
Littorina spp.	2.5	37.8	10.0	90.2	44.1	9.2	43.0	77.6
Turbellaria?	0.7			3.3				
Plant								
Zostera marina		24.4						
Unidentified algae				1.6			5.2	2.6
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

*Specimen 1 collected 21 June; specimen 2 collected 2 July.
†Collected 22 August.

Table 2
Total number and percent of Harlequin Ducks censused in three habitats during pre-nesting–laying (10 May – 21 June), and during post-laying (22 June – 15 August) in Sawmill Bay, Alaska, 1979–1980

	Pre-nesting–laying		Post-laying			
	Pairs		Single males		Single females	
Habitat	*N*	%	*N*	%	*N*	%
Stellar Creek	83	26.4	24	20.5	133	55.4
Rocks	149	47.5	90	76.9	103	42.9
Lee waters	82	26.1	3	2.6	4	1.7
Total	314	100.0	117	100.0	240	100.0

Table 3
Average percent of diurnal time individual Harlequin Ducks spent feeding while in each habitat in Sawmill Bay, Alaska, during pre-nesting–laying (10 May – 21 June), and during post-laying (22 June – 15 August), 1979–80

Period	Habitat	No. of observations	Percent*
Pre-nesting–laying			
Paired males	Stellar Creek	744	19.8[1,2]
	Rocks	974	7.3[3]
	Lee waters	2982	15.0[1]
Paired females	Stellar Creek	744	43.3[1]
	Rocks	937	8.2[3]
	Lee waters	3183	22.4[2]
Post-laying			
Single males	Stellar	771	50.7[1]
	Rocks	2571	1.8
	Lee waters†	—	—
Single females	Stellar	2691	27.3
	Rocks	2082	0.5
	Lee waters†	—	—

*All values are significantly different from each other ($P<0.05$) except those with identical superscripts.
†Single Harlequin Ducks occurred in lee waters only rarely, and feeding rates were not determined for them there.

Table 4
Calculated absolute (and relative) percentages of total diurnal time spent feeding in three habitats by Harlequin Ducks in Sawmill Bay, Alaska, during pre-nesting–laying (10 May – 21 June) and during post-laying (22 June – 15 August), 1979–80

	Pre-nesting–laying				Post-laying			
	Paired males		Paired females		Single males		Single females	
Habitat								
Stellar Creek	5.2*	(41.6)	11.4	(54.0)	10.4	(88.1)	15.1	(98.7)
Rocks	3.4	(27.2)	3.9	(18.5)	1.4	(11.9)	0.2	(1.3)
Lee waters	3.9	(31.2)	5.8	(27.5)	—	—	—	—
Totals	12.5	(100.0)	21.1	(100.0)	11.8	(100.0)	15.3	(100.0)

*Calculated as percent of time spent feeding in each habitat (Table 3) × percent of occurrence of ducks in each habitat (Table 2); e.g. for paired males: $\frac{19.8\% \times 26.4\%}{100} = 5.2\%$.

(27%). However, paired and single males at Stellar Creek exhibited just the opposite pattern (20% *vs* 51%, respectively) (Table 3).

To determine the absolute proportion of total diurnal time that the various segments of the harlequin population spent feeding (Table 4), the habitat-specific feeding rates (Table 3) were multiplied by the proportion of harlequins that occurred in each habitat (Table 2). For all habitats combined, paired females during pre-nesting–laying spent more total time feeding (about 21%) than did paired males during the same period (13%) or than single males and females did during post-laying (12 and 15%, respectively) (Table 4).

Comparing the relative percent of time harlequins spent feeding in each habitat (in parentheses on Table 4) with the percent occurrence of ducks in each habitat (Table 2) we concluded the following:

1. Relative to the amount of time they spent there, harlequins allocated a disproportionately large fraction of their total feeding time to Stellar Creek.

2. Conversely, rocks were under-used for feeding in proportion to the amount of time harlequins spent there.

3. Among paired harlequins, lee waters were used for feeding in about the same proportion as the amount of time they spent in that habitat.

7. Discussion

Harlequins in this study depended on Stellar Creek for nearly half to practically all of their feeding activity. Early in the summer, harlequins fed primarily on marine invertebrates in the intertidal delta of the creek. Later in the summer they moved slightly upstream into the spawning beds of the arriving salmon, where they fed largely on waste, drifting roe. Incubating females flew downstream, at least occasionally, to forage in the outflow or lower portions of the creek (Dzinbal 1982).

This pattern was not unique to Stellar Creek or to Sawmill Bay. Although harlequins hardly used Twin Falls Creek in early summer, after salmon arrived they occasionally foraged along the same few channels used by the salmon. Also, six medium-gradient, non-glacial salmon streams in Valdez Arm had small contingents of harlequins feeding in their outflows or lower reaches, and male harlequins at a moulting site in Valdez Arm regularly fed at the outflow of one such stream (Dzinbal 1982). Osgood (1904) observed that harlequins during summer at Kanatak and Cold Bay on the Alaskan Peninsula "frequently . . . visit the mouths of small streams or . . . ascend them for considerable distances." Also, Bengtson (1972:14) found that harlequins breeding along short, coastal streams in northwest Iceland tended to fly downstream to feed in the river deltas.

Gudmundsson (1971:89) noted that harlequin nesting grounds in Iceland often coincide with Atlantic salmon (*Salmo salar*) spawning grounds, and he suggested that harlequin ducklings and salmon fry may depend upon similar foods. Unlike Atlantic salmon, however, the fry of pink and chum salmon (prevalent in this study) usually do not feed in streams as short as Stellar Creek, but move to the sea the first night following their emergence (Scott and Crossman 1973). Because of their larger size, drifting salmon eggs probably represented a more efficiently exploited food source for harlequins than did invertebrates. Thus, the most likely attraction of the salmon spawning beds for the harlequins in this study was the drifting roe available there. Possibly the low productivity typical of many coastal streams may be offset for harlequins by the seasonal influx of anadromous fish, and by the relative abundance of food in the intertidal stream deltas.

During spring and summer, Harlequin Ducks spent little time feeding, but paired females during pre-nesting and laying fed more often (21%) than other harlequins (12–15%). However, paired female harlequins spent much less time feeding than paired females of six species of dabbling ducks (45–70%; Dwyer 1975, Afton 1979,

Kaminski and Prince 1981). Subtle differences in definition of feeding behaviour may account for some of the reported differences between harlequins and other ducks in the proportion of time spent feeding. Nevertheless, harlequins spent much of their time loafing and preening (~53–74%; Dzinbal 1982) and devoted a relatively small amount of time to searching for and acquiring food. Similarly, Pool (1962:127) only rarely observed harlequins feeding, and noted their "favourite occupation . . . consisted of just sitting around doing nothing."

Ettinger and King (1980) suggested that the large proportion of time Willow Flycatchers (*Empidonax traillii*) devoted to loafing minimized variations in daily energy expenditure between phases of the breeding cycle, and acted as a buffer against periods of stringency (see Wilson [1975:142] for a discussion of stringency). Harlequin Ducks undoubtedly face unpredictable periods of stringency in their storm-prone environment, and possibly their activity patterns have evolved to minimize their energy expenditure rather than to maximize their energy intake. The relatively small proportion of daily time that harlequins spent feeding would be one expected result of such a strategy.

8. Acknowledgements

We especially thank Dirk Derksen and Skipp Ladd for their encouragement and logistical assistance, and Debra Clapp for her help with the field work. Tim Myres, Robert Eng, D.N. Nettleship, Paul Springer, and two anonymous reviewers provided many helpful suggestions on the manuscript, for which we are grateful. Funding for this project was provided by the National Wildlife Federation, National Rifle Association, the US Fish and Wildlife Service (Office of Special Studies, and Office of Migratory Birds, Anchorage, Alaska), and the Society of Sigma Xi. This paper is Oregon Agricultural Experiment Station Technical Paper No. 6276.

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Prey selection by Oldsquaws in a Beaufort Sea lagoon, Alaska

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1. Abstract

The feeding ecology of Oldsquaws (*Clangula hyemalis* L.) was investigated during July–September of 1977–78 in Simpson Lagoon on the Beaufort Sea coast of Alaska. Few species of prey were available. Volumetric analyses of the stomachs of actively feeding birds collected systematically throughout both summers indicated that the diet consisted 70% of two mysids (*Mysis relicta* and *M. litoralis*) and 15% of one amphipod (*Onisimus glacialis*). The remainder of the diet was mainly bivalves. Oldsquaws fed primarily in the portions of the lagoon that ranged from 2 to 3 m in depth, where prey densities were highest. Oldsquaws fed selectively on larger mysids and amphipods, and preyed most effectively (more food found in their stomachs) in areas where prey was most dense and biomass was greatest.

2. Résumé

De juillet à septembre 1977 et 1978, nous avons étudié l'écologie alimentaire des Canards kakawis (*Clangula hyemalis* L.) dans le lagon de Simpson, sur la côte de la mer de Beaufort, en Alaska. Nous avons trouvé peu d'espèces de proies. En effet, d'après l'analyse volumétrique des estomacs des oiseaux qui se nourrissaient activement et qui ont été recueillis systématiquement durant les deux étés, le régime de ces canards se composait essentiellement de 70 % de deux mysis (*Mysis relicta* et *M. litoralis*) et de 15 % d'un amphipode (*Onisimus glacialis*). À cela s'ajoutaient des bivalves. Les Canards kakawis se nourrissaient surtout dans les parties du lagon d'une profondeur de 2 à 3 m où la densité des proies était la plus forte. Ils choisissaient de préférence les mysis et les amphipodes les plus gros et pêchaient plus efficacement (jugé d'après une plus grande quantité de nourriture dans leur estomac) dans les zones où les proies étaient les plus denses et la biomasse, supérieure.

3. Introduction

Tens of thousands of male Oldsquaws and a small number of non-breeding females congregate in nearshore Beaufort Sea lagoons during July and August (Johnson and Richardson 1982). In contrast, breeding female Oldsquaws remain with their broods on freshwater tundra lakes and ponds, often until ice forces them to leave these for the coastal lagoons in mid to late September. This paper describes the feeding relationships between Oldsquaw ducks (*Clangula hyemalis*) and their invertebrate prey in Simpson Lagoon, one of a series of shallow lagoons on the north coast of Alaska (Fig. 1).

The main purpose of this study was to determine which prey organisms formed the important components of Oldsquaw diets in the study area, and to determine the relationship between prey availability and prey selection by feeding Oldsquaws. Investigations of the feeding ecology of marine birds provide a key link in the interpretation of the relationship between biological productivity and abundance of birds. The studies of Oldsquaws were part of a larger interdisciplinary study of ecological processes (LGL 1981).

4. Methods

4.1. Collection of birds and habitat samples

The procedures for collecting Oldsquaws and Oldsquaw feeding habitat samples during 1977 were the following:

1. A flock of Oldsquaws was located and watched for 3–5 min to determine whether some birds appeared to be feeding by diving. An estimate was made of the flock size.

2. Observers then sped into the flock by boat (4.9-m Zodiac with 35-hp outboard), dropped an anchored buoy into the water as the vessel slowed, and shot as many birds as possible (generally three to eight individuals).

3. Birds were retrieved and labelled. To mitigate post-mortem digestion, the esophagus, proventriculus, and gizzard were injected immediately with absolute isopropyl alcohol. The esophagus was then plugged with paper.

4. Habitat sampling occurred after the collecting party returned to the buoy.

a. For each set of birds collected, two zooplankton samples were obtained, one from the surface water and another from the mid-water column. This was accomplished by towing both a surface-supported 14-by-10-cm neuston net (mesh size 0.079 mm) and a submerged (1-m deep) 0.25-m diameter macroplankton net (mesh size 0.239; see Griffiths and Dillinger (1981) for more details of sampling equipment).

b. One sample from the lagoon epibenthos (bottom community) was collected. From a stationary boat in the area of the buoy the 0.25-m macroplankton net was towed manually across the bottom of the lagoon for a distance of approximately 10 m at a speed of approximately 0.5–1.0 m/s. The water depth at this location was measured with the buoy rope. Observations by SCUBA divers in this study indicated that the epibenthic community in Simpson Lagoon extended from the bottom surface upward to about 0.25–0.75 cm and included a suspension of detrital material several centimetres thick. The 0.25-m macroplankton net was a relatively crude device for sampling the epibenthos;

no doubt many fast-moving organisms (e.g. mysids) escaped from the net before it could be retrieved. The net often bounced along the bottom and scraped a thin layer of mud and accompanying infaunal organisms from the top 1 cm of bottom substrate.

c. Habitat samples were washed immediately from the sampling nets and preserved in 10% neutral Formalin.

During 1977, 31 collections of Oldsquaws ($\bar{x}$ = 2.8 birds/collection; total = 87) were made in Simpson Lagoon from 11 July through 14 September. During 1978, 45 collections ($\bar{x}$ = 2.4 birds/collection; total = 108) were made in Simpson Lagoon from 10 July to 27 September. The same general procedures for collecting Oldsquaws were followed in both 1977 and 1978. Prior to making collections in 1978, however, some flocks were watched more carefully and longer (10–30 min) to determine whether they appeared to be feeding. Of the 81 feeding birds that were collected in 1978, 65 (80%) had identifiable food in their stomachs, whereas of the 27 birds that were taken indiscriminately with no prior observations of behaviour, only 7 (26%) contained some identifiable food. During 1977, 54 (62%) of the Oldsquaws collected had identifiable food in their stomachs; that proportion was similar to the overall value for the 1978 collections (67%). Thus, optimum use and least wastage of Oldsquaw specimens depends on adequate observation to determine that the birds are actively feeding and will be useful in prey analyses.

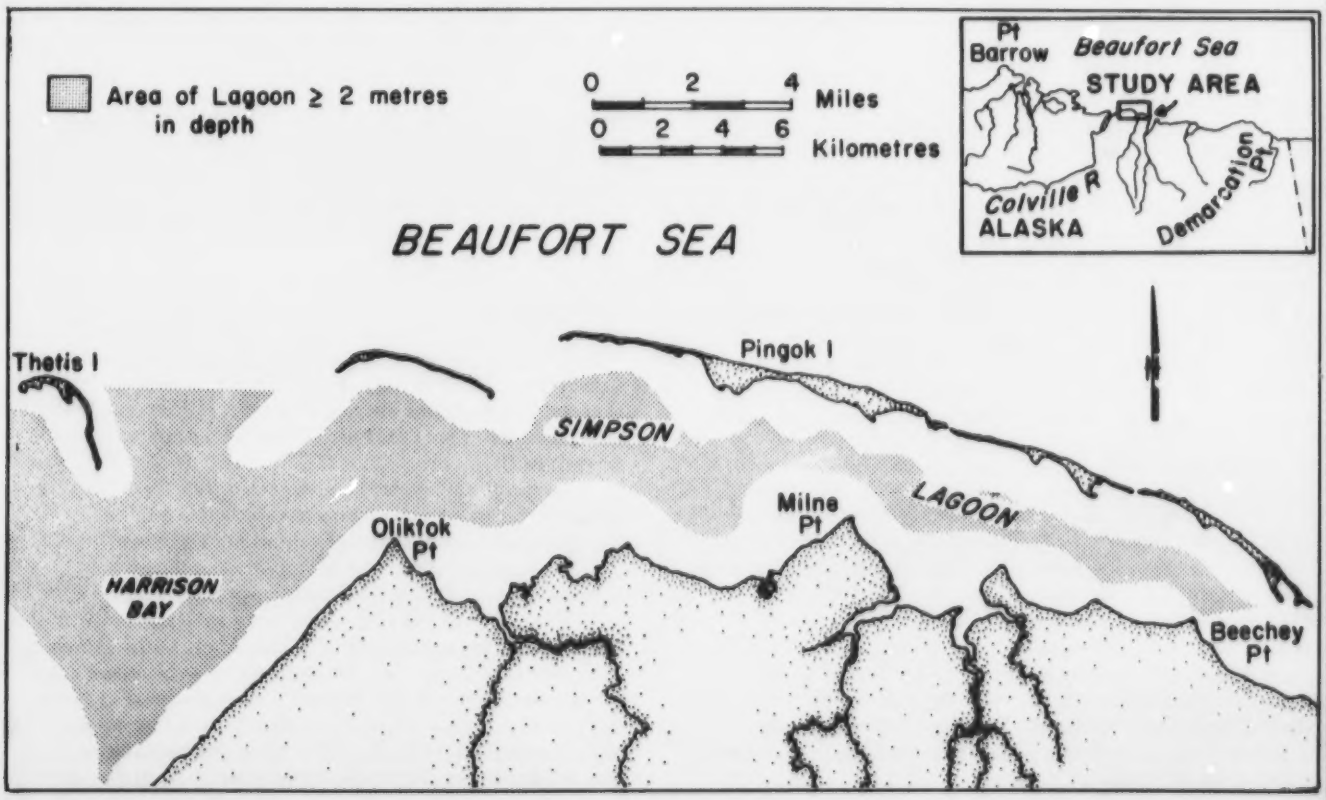
Studies during 1977 (Griffiths and Dillinger 1981, Johnson and Richardson 1981) indicated that Oldsquaws fed primarily on epibenthic invertebrates and bivalves found on or near the lagoon bottom. Therefore, during 1978, samples for analyses of food availability were collected only from this level of the lagoon. To minimize escapement of mobile epibenthic animals, the drop-net method (mesh 1.0 mm; Fig. 2) of Griffiths and Dillinger (1981) was substituted in 1978 for the 0.25-m macroplankton net tows. The drop net sampled from the bottom surface of the lagoon (including approximately 1 cm of substrate) and also from the bottom 95 cm of the water column. Three to five drop-net samples were collected immediately at each location where birds were collected.

4.2. Laboratory techniques

Within 24 h of collection all birds were dissected in a field laboratory and food items were preserved. The esophagus, proventriculus, and gizzard were removed as a single unit from each bird. During 1978 this unit was slit lengthwise, and an arbitrary measure of fullness (Hynes 1950, Griffiths *et al.* 1975; see below) was assigned to the total unit. A cursory and tentative description of the contents was also recorded. These contents were then washed with 10% neutral Formalin into a 227-mL bottle for later reexamination. During 1977 no measure of fullness was assigned in the field, but all other procedures were the same.

To assess and compare the importance of various invertebrate taxa in the diet of Oldsquaws in 1977 and 1978, the preserved stomach contents were sorted by trained invertebrate zoologists, and an estimate was made of the

Figure 1
Simpson Lagoon, Alaska



relative volume of each major taxon (e.g. amphipod, mysid, copepod, isopod, and so on) following the procedures developed by Hynes (1950) and modified by Griffiths *et al.* (1975). Twenty points were assigned to the fullest Oldsquaw stomach analysed. The fullness of each other stomach was subsequently gauged against the fullest stomach, and a corresponding number of points were assigned. After the sample had been sorted, and after each major taxon had been bottled, the total number of points thus assigned to each stomach was partitioned among the major invertebrate taxa present according to the relative volume of each. No distinction was made between whole organisms and fractions thereof. Pieces of unidentified organisms were classified as such.

During 1977 and 1978, each habitat sample was sorted and bottled by major taxon. Twenty points were assigned to the total volume of each sample, and then an estimate of the relative proportions (volumes) of the total 20 points was assigned to the various major taxa in the sample.

During 1977 the two most important taxa (mysids and amphipods) present in the stomachs and habitat samples were sorted further, identified to the species level, and weighed (Formalin wet weight). For a size comparison, 20 individuals each of mysids and amphipods were selected randomly from each Oldsquaw stomach and from its associated habitat samples; these individuals were measured to the nearest millimetre. During 1978 a much more detailed system of sorting and measuring was adopted; all individuals present in the stomachs and habitat samples were sorted to major taxa, identified to the species level, counted, weighed, and measured.

No studies were conducted to determine if the contents of the esophagus, proventriculus, and gizzard differed significantly. Therefore, as shown by Bartonek (1968), Bartonek and Hickey (1969), and Swanson and Bartonek (1970), some bias in prey analysis may have resulted because of differential digestion in these portions of Oldsquaw digestive tracts. Very few soft-bodied invertebrates were found in Oldsquaw digestive tracts or their feeding habitat (epibenthos), however, and our detailed laboratory analyses in 1978 confirmed that the broken shells of bivalves and the telsons and adjacent urosomes of mysids and amphipods remained identifiable and measurable in Oldsquaw gizzards. Reference collections were made of all Oldsquaw prey organisms, and regression equations were developed to relate the partial length of incompletely digested invertebrate organisms to total length, weight, and caloric value of whole organisms of the same species. Further details of the identifying, sorting, counting, weighing, and measuring procedures followed during 1977 and 1978 are described in Griffiths and Dillinger (1981).

All results presented are of the total seasonal diets of Oldsquaws. Cluster analyses (see Clifford and Stephenson 1975:134 for procedures) indicated no justification for further, more detailed categorizations of early, middle, and late season diets of Oldsquaws.

5. Results

5.1. Oldsquaw diet

Of the 87 Oldsquaws collected during 1977, 15 had empty stomachs and 18 contained only unidentifiable material. The average diet of the remaining 54 birds included, on a percent estimated volume basis, 58.7% mysids, 14.2% amphipods, 8.1% bivalves, 2.3% isopods, 2.3% small fishes, and 14.2% unidentifiable material (Table 1).

The Oldsquaw diet during 1978 was similar to that in 1977 (Morisita Similarity Index, $\bar{C} = 0.74$; Horn 1966). Of the 108 Oldsquaws collected during 1978, 34 had empty stomachs and 2 contained only unidentifiable material. The average diet of the remaining 72 birds, on a percent estimated volume basis, was 68.5% mysids, 15.5% amphipods, and 12.1% bivalves (Table 1). Unidentifiable material comprised a much smaller portion of the stomach contents in 1978 (1.5%) than in 1977 (14.2%) because of the availability of completed reference collections and improved identification procedures in the second year of study.

Table 2 provides a comparison of the proportions of major taxa found in Oldsquaw stomachs as determined by precise measurements of wet weight, ash-free dry weight, energy content (kilocalories), and abundance (total individuals) as well as by the qualitative, modified Hynes Point method. The Hynes Point method proved to be a relatively accurate indicator of the proportion and importance of various major taxa of prey organisms consumed by Oldsquaws. Percentages computed from Hynes Point values were almost identical and were not significantly different ($P > 0.05$) from percentages computed from ash-free dry weight and energy content values (see Table 2).

The main prey species were the mysids *Mysis litoralis* and *M. relicta*, the amphipod *Onisimus glacialis*, and the bivalves *Portlandia arctica* and *Cyrtodaria kurriana* (Table 3).

5.2. Prey availability

Gear used for surface and mid-water collections in 1977 probably provided a reasonably accurate indicator of prey availability there, but epibenthic invertebrates of the

Table 1
Percentage volumetric comparison of Oldsquaw diet in relation to composition of epibenthic samples from Simpson Lagoon

	1977		1978	
Prey	Oldsquaw diet ($N = 54$; total points* = 443)	Epibenthic samples ($N = 18$; total points = 160)	Oldsquaw diet ($N = 72$; total points = 422)	Epibenthic samples ($N = 39$; total points = 166⅓)
Mysids	58.7	28.1 (42.5)†	68.5	48.9
Amphipods	14.2	27.5 (41.5)	15.5	36.6
Bivalves	8.1	1.9 (2.8)	12.1	7.1
Isopods	2.3	0	1.0	1.4
Fishes	2.3	0	0.2	0.3
Copepods	0.1	33.8 —	0.2	0.5
Polychaetes	0	1.9 (2.8)	0.7	2.4
Euphausiids	0	0	0.2	0
Priapulids	0	0	0.1	1.1
Tunicates	0	0	0.1	0.6
Cnidarians	0	2.5 (3.8)	0	0.8
Pteropods	0	3.1 (4.7)	0	0
Ostracods	0	0.6 (0.9)	0	0
Foraminiferans	0	0.6 (0.9)	0	0
Sponges	0	0	0	0.1
Chaetognaths	0	0	0	0.1
Cumaceans	0	0	0	0.1
Unidentifiable	14.2	0	1.5	0
Total	99.9	100.0	100.1	100.0

*See Griffiths *et al.* (1975) for a description of the points method for assessing the relative importance of food organisms.
†Recomputed percentages after omitting copepods, whose appearance in epibenthic samples may have been an artifact of the sampling method.

types important to Oldsquaws were especially difficult to sample quantitatively. Methods used to sample such animals in 1978 were much improved over those used in 1977. These problems must be recognized when interpreting the data concerning food availability.

Few mysids or amphipods were collected from the surface waters of the lagoon (Fig. 3). This evidence, plus our observations and published information (see Discussion) on the diving behaviour of Oldsquaws, indicated that Oldsquaws probably rarely feed in this layer. The predominant invertebrate taxa present in this layer during 1977 were, on an estimated percent of total volume basis, copepods (68.1%) and cnidarians (16.7%). Most of the remainder of the organisms collected in this habitat were amphipods (5.7%) and chaetognaths (3.3%).

Copepods represented almost two-thirds (64.4%) of the total volume of invertebrate organisms present in the mid-water habitat samples (Fig. 3); this proportion was similar to that found in the surface water samples. Mysids and amphipods comprised 11.7 and 9.4%, respectively, of the mid-water samples. Cnidarians, chaetognaths, and ctenophores represented a major proportion of the remainder of the mid-water samples during 1977.

Copepods, mysids, and amphipods comprised the major proportions (33.8, 28.1, and 27.5%, respectively) of the epibenthic samples collected during 1977 (Table 1). Observations by a SCUBA diver at several locations in Simpson Lagoon during 1977 and 1978, indicated that mysids and amphipods were the most conspicuous invertebrate organisms present in the epibenthos (Griffiths and Dillinger 1981). The relatively large volume of copepods in the "epibenthic" samples taken during 1977 was probably an artifact of the sampling equipment (0.25-m

Figure 2
Shallow water drop net used to sample invertebrates in Simpson Lagoon

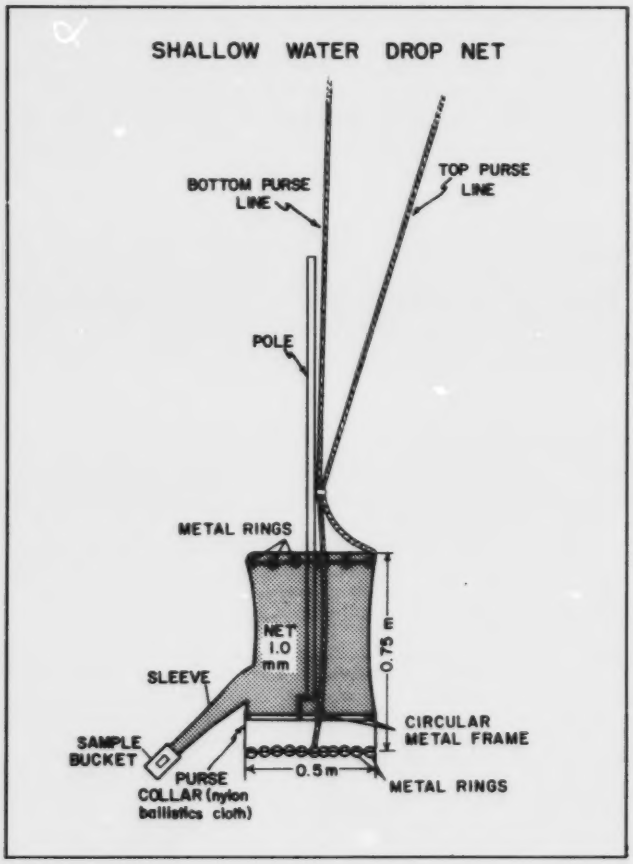


Table 3
Identifiable prey consumed by Oldsquaws in Simpson Lagoon*

Prey	1977 Oldsquaws (*N* = 54)	1978 Oldsquaws (*N* = 72)
Mysids		
Mysis litoralis and *M. relicta*	67.6	79.7
Amphipods		
Onisimus glacialis	8.0	10.4
Parathemisto spp.	4.9	0.3
Gammarus setosus	1.7	0.8
Gammaracanthus loricatus	1.2	0.7
Apherusa glacialis	<0.1	—
Pontoporeia affinis and *P. femorata*	—	<0.2
Bivalves		
Cyrtodaria kurriana	7.1	5.1
Portlandia arctica	2.4	1.1
Isopods	2.7	0.9
Fishes	2.7	0.4
Copepods	1.2	<0.1
Cumaceans	—	0.1
Euphausiids	—	0.1
Polychaetes	—	0.1
Others	—	0.3
Total	99.7	100.3

*Presented as percent composition (wet weight).

Table 2
Diet of Oldsquaws in Simpson Lagoon during 1978 as determined by various measures

	Volume		Abundance		Wet weight		Ash-free dry weight		Energy content	
Prey	Points*	%	No.	%	g	%	g	%	kcal	%
Mysids	289	68.5	6464	75.0	155.1	77.4	17.9	69.7	97.5	69.8
Amphipods	65¼	15.5	1845	21.4	23.7	11.8	4.2	16.3	21.3	15.3
Bivalves	51¼	12.1	260	3.0	13.3	6.6	2.6	10.1	14.7	10.5
Other taxa	16½	3.9	48	0.6	8.3	4.1	1.0	3.9	6.1	4.4
Total	422	100.0	8617	100.0	200.4	99.9	25.7	100.0	139.6	100.0

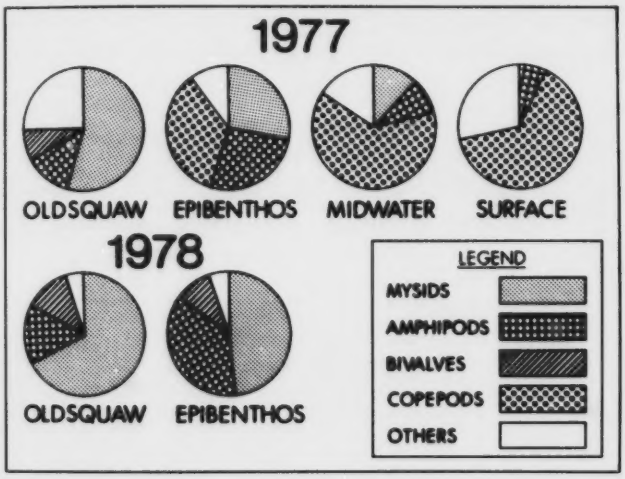
*See Griffiths *et al.* (1975) for a description of the points method for assessing the relative importance of food organisms. Points listed in this table are only those of identifiable taxa.

macroplankton net); they presumably were taken in the water column as the net sank and was retrieved.

Because both mysids and amphipods, the organisms that comprised the major proportions of the diet of Oldsquaws during 1977, were proportionately most abundant in the lagoon epibenthos, oldsquaws probably fed almost exclusively from this habitat rather than from either the surface or the mid-water layers where mysids and amphipods were relatively uncommon. The few copepods in the diet of Oldsquaws during 1977 may have been taken incidentally during the process of feeding on other epibenthic invertebrates (Table 1, Fig. 3).

Mysids and amphipods collectively represented 85.5% of the estimated volume of invertebrates in the 1978 epibenthos samples. Although the drop-net sampling technique was not designed as an infaunal sampler, a notably larger proportion of the estimated volume of epibenthic samples consisted of bivalves in 1978 (7.1%) than in 1977 (1.9%). Differences in wet weights of bivalves in 1977 (9.5%) and 1978 (6.2%) were not as marked, however (Table 3). Perhaps because more effective sampling gear was used during 1978, the relative importance of copepods in the epibenthos was markedly lower in 1978 (0.5% of estimated volume) than in 1977 (33.8%).

Figure 3
Volumetric composition of Oldsquaw diets and feeding habitat samples in Simpson Lagoon



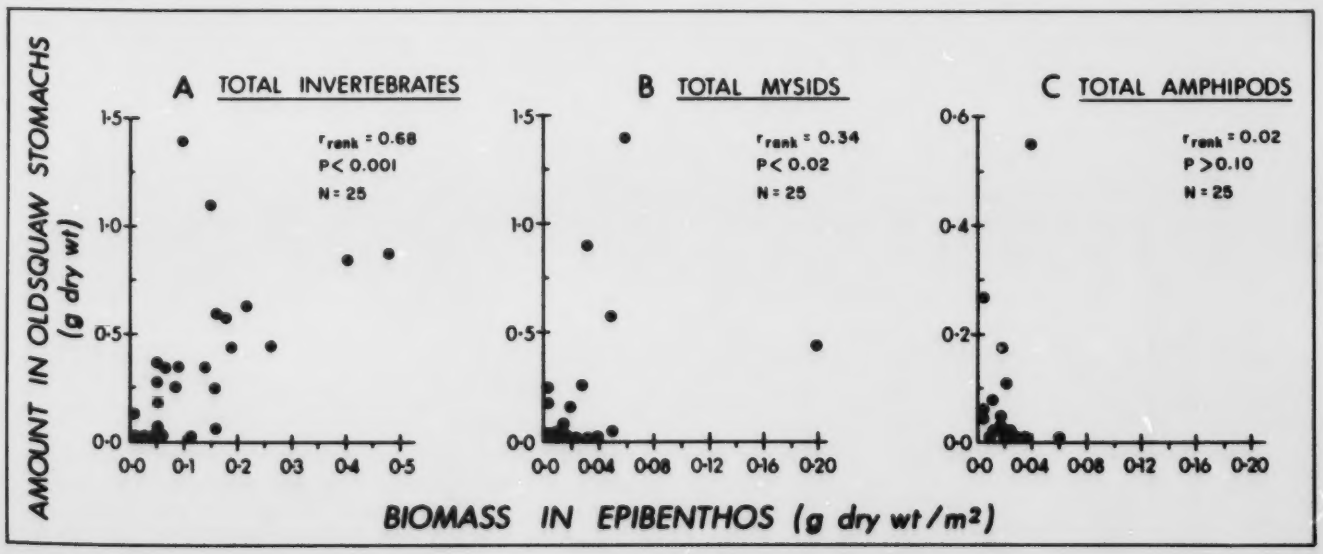
5.3. Selectivity in diet

The results from 1978, when more effective epibenthic sampling gear was used, show a generally close relationship between the relative volumes of major invertebrate taxa in Oldsquaw stomachs and in the epibenthic habitats (Table 1, Fig. 3). Furthermore, the weights of invertebrates as a group, and of mysids in particular, in the stomach contents of individual Oldsquaws were positively and significantly correlated with the availability of these animals in the epibenthos at the place and time of collection (Fig. 4). However, diet was not totally parallel to food availability. In both 1977 and 1978 the relative proportions of mysids found in Oldsquaw stomachs were substantially greater than those found in feeding habitats (Table 1). The differences in 1977 between mysids in the diet and in the epibenthos remain large even if copepods are not considered in the epibenthos percentage computations.

In contrast to the mysids, the weights of amphipods in the stomachs in 1978 showed no positive or significant correlation with the availability of these animals in the epibenthos (Fig. 3). During both 1977 and 1978, the proportions of amphipods in Oldsquaw stomachs were about half those found in feeding habitats (Table 1).

Data from both 1977 and 1978 indicate that, on the basis of the total season diet, the average sizes of mysids and amphipods consumed by Oldsquaws were significantly larger than the average sizes of the same species found in the epibenthos (Table 4; Fig. 5). Hence, in Simpson Lagoon,

Figure 4
Relationship in Simpson Lagoon in 1978 between amount of prey in stomachs of feeding Oldsquaws and the biomass of prey in the epibenthos where feeding Oldsquaws were collected



feeding Oldsquaws apparently tended to select larger individuals of at least the most common prey species, especially mysids, found in epibenthic feeding habitats. In 1978, this selection by Oldsquaws of the large size classes of invertebrates is most apparent during mid July for all major prey consumed, and is less apparent later in the season, especially for *Mysis litoralis* (Table 5).

6. Discussion

Oldsquaws in Simpson Lagoon, as at other locations, are largely opportunistic feeders — they prey on organisms in accordance with their availability. In coastal wintering areas in North America (Stott and Olson 1973; Vermeer and Levings 1977, Sanger and Jones 1981), as in Europe (Madsen 1954, Nilsson 1972, Bagge *et al.* 1973), Oldsquaws feed extensively on those organisms that are most abundant, primarily epibenthic crustaceans and molluscs. Gjosaeter and Saetre (1974) reported Oldsquaws and eiders feeding extensively on the eggs of capelin (*Mallotus villosus*) during the spawning season of this fish in the Barents Sea.

In freshwater habitats also, Cottam (1939), Bengtson (1971), and Pehrsson (1974) showed that abundant crustaceans comprise a major proportion of the diet of Oldsquaws. Lagler and Wienert (1948) reported crustaceans and molluscs to be important prey of Oldsquaws at locations in Lake Michigan where Eggleton (1936) had earlier found the greatest abundance of these invertebrates. An analysis of stomachs of Oldsquaws taken from gill nets in Lake Michigan showed them to be opportunistic in their feeding behaviour. There was a close relationship between the prey items in groups of ducks taken in the same haul of nets; therefore it was concluded that the Oldsquaws were simply utilizing, on a non-selective basis, whatever food resources were available in the area in which they were taken (R.S.

Table 4
Comparison of the sizes of the most important marine invertebrates taken from Oldsquaw stomachs and from the epibenthos in Simpson Lagoon

Prey species	Prey length in Oldsquaw stomach, mm	Prey length in epibenthic sample,* mm	*N*	Z†	*P*<
1977					
Mysis litoralis	13.3 ± 2.6‡	10.7 ± 3.4	20	1.97	0.06
Mysis relicta	12.7 ± 1.4	10.6 ± 1.5	20	2.91	0.01
Onisimus glacialis	5.6 ± 1.2	4.4 ± 1.7	20	2.35	0.03
1978					
Mysis litoralis	12.4 ± 2.2	8.9 ± 3.5	20	2.89	0.01
Mysis relicta	12.1 ± 1.9	8.8 ± 2.1	20	2.61	0.02
Onisimus glacialis	5.8 ± 1.0	4.2 ± 0.8	20	2.94	0.01

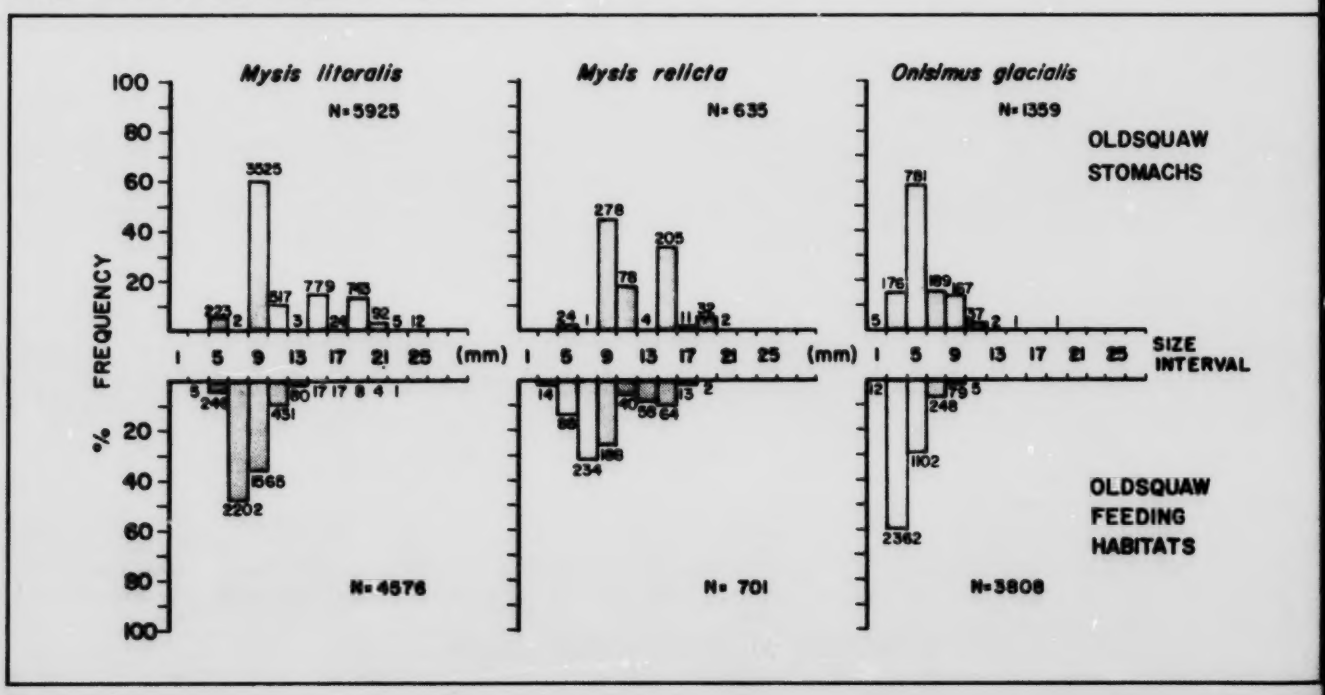
*Epibenthic samples were collected at the locations where birds were collected.
†Wilcoxon's matched-pairs tests.
‡Mean ± standard deviation.

Table 5
Comparisons of sizes of prey available and eaten by Oldsquaws in Simpson Lagoon during 1978

Prey species	Overlap index* for various sampling periods			
	Mid July (*N* = 8–14)†	Early August (*N* = 5–12)	Mid August (*N* = 5–13)	Late August (*N* = 10–13)
Mysis litoralis	0.12	0.09	0.82	0.83
Mysis relicta	0.21	0.64	0.85	0.71
Onisimus glacialis	0.37	0.65	0.75	0.82

*Morisita Overlap Index (Horn 1966).
†*N* = range in number of stomachs compared.

Figure 5
Distribution of sizes of prey in the stomachs of feeding Oldsquaws and in the epibenthos where feeding Oldsquaws were collected



Ellarson, pers. comm. 1982). In northern Sweden, Pehrsson (1973) found that both female Oldsquaws with broods and other post-breeding Oldsquaws selected and were concentrated on lakes that supported high densities of euphyllopod crustaceans. Hull (1914) and Ellarson (1956:215) recorded Oldsquaws feeding on locally abundant minnows in Lake Michigan.

The relationship between Oldsquaws and their benthic prey in Simpson Lagoon is remarkably similar to that in portions of Lake Michigan. In Simpson Lagoon the principal prey of Oldsquaws consisted of two species of mysids, two amphipods, and two bivalves. The two mysids and *Onisimus glacialis* are epibenthic-dwelling crustaceans. In Simpson Lagoon and many other lagoons along the Beaufort Sea coast these crustaceans are associated with a detrital suspension several centimetres thick on the lagoon bottom (Griffiths and Dillinger 1981).

In Lake Michigan, Peterson and Ellarson (1977) found the primary prey to be a single species of epibenthic amphipod (*Pontoporeia affinis*; 82% of winter diet). Furthermore, they found that Oldsquaws concentrated to feed in the same areas where *Pontoporeia affinis* reached maximum density. Field experiments in Lake Michigan by Marzolf (1962, in Peterson and Ellarson 1977) indicated that a thin detrital film (less than 5 mm) was generally present on the bottom of the lake. His laboratory experiments also suggested that *Pontoporeia* densities were positively correlated with the density of bacteria in this organic matter. Although Schell (1980) found no such relationship between the common invertebrates (e.g. mysids and *Onisimus*) living in Simpson Lagoon and peat-associated bacteria, further study of other types of detritus and bacteria may show a relationship in Simpson Lagoon similar to that described by Marzolf (1962) in Lake Michigan.

The standing stock of benthic infauna (bivalves, polychaetes, cumaceans, tunicates, and other organisms) in Simpson Lagoon substrates is at least as high as that of the mobile epibenthos (2.2 g *vs.* 0.1–2.5 g ash-free dry wt/m^2; Griffiths and Dillinger 1981). Nevertheless, only 10% or less of the diet of Oldsquaws in Simpson Lagoon was found to be composed of bivalves (primarily *Cyrtodaria kurriana* and, to a lesser extent, *Portlandia arctica*), cumaceans, and polychaetes (Table 3). Some of these organisms may have been available in the epibenthos (H. Feder, Univ. of Alaska, pers. comm. 1981), so the percentages of the diet represented by infaunal organisms may have been even lower.

In Milwaukee Harbor in Lake Michigan, infaunal oligochaetes (Tubificidae) were very abundant in winter (up to 335 000/m^2; Rofritz 1972:56) and were almost the exclusive diet of most Oldsquaws, even though molluscs and crustaceans were also present in the benthos where the birds were feeding (Rofritz 1977). It was suggested that Oldsquaws in Milwaukee harbour may have selected oligochaetes as food during winter because of their significantly higher caloric value per gram of body weight than the other benthic fauna present. Oligochaetes were absent, however, from the diet of some Oldsquaws. These worms may have been in burrows in the sand and silt substrate during some periods and at some locations, and therefore may have been largely inaccessible to some Oldsquaws.

My results suggest that Oldsquaws select the larger mysids and amphipods, and prey most effectively in areas where the density and biomass of food are high (Figs. 4 and 5). Griffiths and Dillinger (1981), in systematic samples at shallow and deep stations in Simpson Lagoon that were established independently of the presence or absence of Oldsquaws, showed that the density of invertebrates was not homogeneous. They found that densities of both mysids and amphipods were significantly greater at their deep ($\bar{x}$ = 2.5 m) lagoon sampling stations in the central trough near the middle of Simpson Lagoon than elsewhere. Average depths where Oldsquaws were feeding and were collected in Simpson Lagoon during both 1977 and 1978 ranged from 2 to 3 m, namely, in the area where densities of lagoon invertebrates were highest.

We have not investigated rates of predation by Oldsquaws. This aspect of the functional feeding response is an important one because it no doubt would be affected by changes in the density of invertebrates. If dramatic reductions in invertebrate density should occur because of oil pollution (see Cabioch 1980, Berne *et al.* 1980), Oldsquaws and other organisms dependent on invertebrates for food may be forced to: (1) move to a more suitable area, or (2) increase their searching time, thus becoming less efficient. We know little of the local movements of flocks of Oldsquaws. Turnover rates of individuals within flocks or of flocks within a lagoon system are not well understood.

Nilsson (1970) indicated that Oldsquaws he observed wintering along the coast of south Sweden during 1964–67 spent approximately 79% of daylight hours diving and that the rate of feeding increased as the ambient temperatures along the coast decreased. Thus, Oldsquaws are capable of functional changes in their feeding behaviour in response to some types of natural perturbations. It remains to be seen, however, whether these seaducks can adapt to the increased disturbance and development-related alterations of their lagoon habitats along the Beaufort Sea coast of Alaska.

7. Acknowledgements

Our work on Oldsquaws in the Alaskan Beaufort Sea (Johnson and Richardson 1981) was supported through the Outer Continental Shelf Environmental Assessment Program (OCSEAP) of the National Oceanic and Atmospheric Administration (NOAA), US Department of Commerce, and the Bureau of Land Management (BLM), US Department of Interior. The support of the OCS Arctic Project Office helped ensure that our research was successful.

Many people at LGL helped in the field and office. In particular, LGL studies of fish and invertebrates in Simpson Lagoon were relevant to the Oldsquaw studies, and I have therefore referred to some aspects of the methods and results of these other studies. My thanks go to Chip Welling, William Griffiths, Peter Craig, Lew Haldorson, Howard McElderry, Rob Dillinger, and Gary Searing.

John Richardson, Chip Welling, Declan Troy, William Griffiths, Dale Herter, and Dave Barnard of LGL; Paul Springer and Margaret Petersen of the US Fish and Wildlife Service; and M.T. Myres of the University of Calgary kindly reviewed earlier versions of this manuscript; their constructive comments helped a great deal. Debbie Whitford and Evelyn Kimbrough typed the manscript, and Diane Hollingdale and Betsy Sturm prepared the illustrations.

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Winter feeding ecology and trophic relationships of Oldsquaws and White-winged Scoters on Kachemak Bay, Alaska

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1. Abstract

The feeding ecology of Oldsquaws (*Clangula hyemalis*) and White-winged Scoters (*Melanitta deglandi*) was studied on Kachemak Bay from November 1977 through April 1978. These species form the bulk of a large wintering waterfowl population. Oldsquaws were extreme generalists, eating at least 61 prey species. The most important were the Pacific sandlance (*Ammodytes hexapterus*), Stimpson's surf clam (*Spisula polynyma*), and blue mussel (*Mytilus edulis*). Scoters were generalists on molluscs, mostly bivalves. They ate at least 22 prey species; the most important were the common Pacific littleneck clam (*Protothaca staminea*), blue mussel, and puppet margarite snail (*Margarites pupillus*). There was little overlap in kinds of prey between the two ducks, and when it occurred the scoters ate significantly larger prey. On the basis of birds observed and collected and the known habitats of their prey species, both sea ducks presumably foraged in water less than 20 m deep, Oldsquaws mostly over substrates of sand and mud, and scoters mostly over bottoms of shell debris and cobbles. The base of the food web in Kachemak Bay depends on the production and availability of organic detritus. Little is known about ecological processes between production of detritus and the production and availability of the birds' filter- and deposit-feeding prey. However, both ducks apparently function as first- to fourth-order carnivores, depending upon which prey species they eat.

2. Résumé

De novembre 1977 à avril 1978, nous avons étudié l'écologie alimentaire des Canards kakawis (*Clangula hyemalis*) et de la Macreuse à ailes blanches (*Melanitta deglandi*) dans la baie de Kachemak. Ces espèces forment la majeure partie de la vaste avifaune hivernante. Les Canards kakawis ont un régime extrêmement opportuniste, comprenant au moins 61 espèces. Les plus importantes étaient : le lançon gourdeau (*Ammodytes hexapterus*), la palourde de Stimpson (*Spisula polynyma*) et la moule bleue (*Mytilus edulis*). Les macreuses se nourrissent indifféremment de mollusques, surtout de bivalves. Leur régime se composait d'au moins 22 espèces. Les plus importantes étaient : le protothaca du Pacifique (*Protothaca staminea*), la moule bleue et la margarite pupille (*Margarites pupillus*). Nous avons constaté très peu de concurrence pour les espèces consommées entre les deux canards, mais, le cas échéant, les macreuses capturaient des proies significativement plus grosses. Si on en juge par les oiseaux observés et recueillis et les habitats connus de leurs proies, ces deux canards de mer puiseraient leur nourriture à des profondeurs inférieures à 20 m : les Canards kakawis, dans les eaux couvrant des substrats de sable et de boue, et les macreuses, sur des fonds de débris de coquillages et de cailloux roulés. Le réseau trophique dans la baie de Kachemak repose sur la production et la disponibilité de détritus organiques. Nous savons très peu de choses sur les processus écologiques intervenant entre l'accumulation de détritus et la production et la disponibilité des proies se nourrissant par filtration ou de dépôts. Nous savons cependant que ces deux canards agissent apparemment comme carnivores de premier à quatrième ordre, tout dépendant de l'espèce de proie qu'ils consomment.

3. Introduction

Kachemak Bay, near the mouth of Cook Inlet in southcentral Alaska (Fig. 1), has high biological productivity, and important commercial fisheries and recreational uses (Trasky *et al.* 1977). Erikson (1977) conducted surveys of marine birds on the bay in 1976 as part of broad-based environmental studies of adjoining Cook Inlet (Trasky *et al.* 1977). He discovered that over 90% of the marine birds in lower Cook Inlet in winter were in Kachemak Bay and that most of these were waterfowl. J.H. Crow (unpubl. data) studied the foods of marine ducks shot by hunters in the China Poot Bay area of Kachemak Bay during September–November 1977, and David Erikson (unpubl. data) collected sea ducks for food studies in spring 1976 in the inner bay. The feeding habits of wintering birds remained essentially unknown, however.

In order to fill this gap, we studied the feeding ecology of the main species of marine-associated birds wintering on the bay. The primary objectives were to determine the kinds, amounts, and trophic levels of prey used by the main species of birds and to relate these findings to the physical and biological environment of the bay. A secondary objective was to make general observations of the distribution and feeding behaviour of the birds. This paper concerns the feeding ecology of the two main species of sea ducks, the Oldsquaw (*Clangula hyemalis*) and White-winged Scoter (*Melanitta deglandi*). Other species of waterfowl were present, but none were consistently present in areas that we could reach safely in our open skiff.

4. Description of study area

Kachemak Bay is a major geographic feature of the Kenai Peninsula and Cook Inlet in southcentral Alaska (Fig. 1). It is 38 km wide at its entrance and about 62 km long. Homer Spit projects 7 km into the bay, dividing it into

physically and biologically distinct "inner" and "outer" bays. The north shore of the bay is unbroken by inlets, but the south side has several islands, fiords, and shallow bays. The mean diurnal tide range is 4.7 m (Trasky *et al.* 1977).

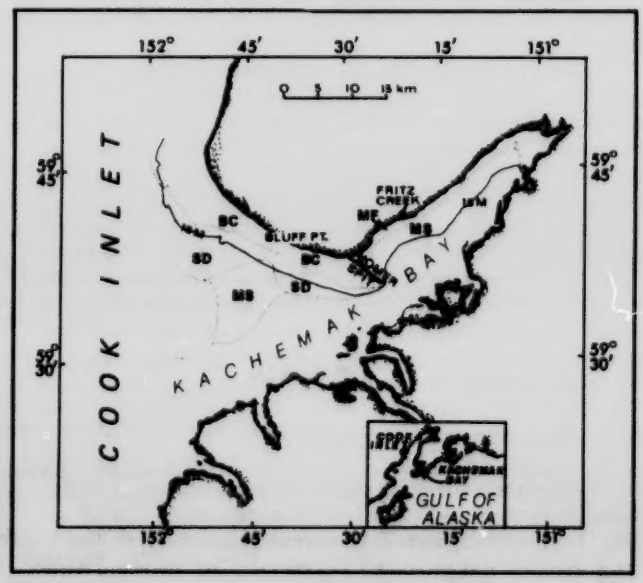
In the inner bay, scattered boulders occur on extensive mud flats immediately adjacent to shore and on the sand and mud bottom just beyond (Fig. 1) (Lees and Driskell 1981). Blue mussels (*Mytilus edulis*) and other biota encrust the boulders, which thus constitute rocky microhabitats. Clays originating from glacial streams at the head of the bay and from erosion of bluffs extend from there to a depth of 18 m.

In the northern outer bay, areas shallower than 9 m are more subject to tidal currents than those in the inner bay, and substrates are markedly different. Boulders and cobbles predominate in depths less than 18 m. From there to the 37-m depth contour the substrate is shell debris, muddy sand, or rippled sand. Water depths away from shore in both the inner and outer bays range mostly from about 35 to 90 m.

Most water in Kachemak Bay originates from coastal upwelling just off southernmost Kenai Peninsula (Burbank 1977, Trasky *et al.* 1977). Surface water flows into the south side of the outer bay from Cook Inlet, and a net northwest current flows out of the bay along the north shore. Drogue studies suggest that the same water can remain in the outer bay for several days before moving out of it (W.P. Wennekens, pers. commun.). Water enters the inner bay from the outer bay at subsurface depths and from streams at the head of the bay. Circulation patterns directly influence the transport of mineral sediments and organic detritus, and sedimentation affects substrate type and thus the nature of benthic animal communities. Organic detritus is believed to form the base of the Kachemak Bay ecosystem (Lees and Driskell 1981).

Ice can build up considerably in the shallow inner bay behind Homer Spit. During this study we encountered moderate amounts of pan and brash ice from December to March in the inner bay between the spit and Fritz Creek (Fig. 1). Ice scouring of the bottom can adversely affect the benthos (Lees and Driskell 1981), thus directly influencing the distribution of the birds' prey. Air temperatures in winter are generally below freezing; during this study they ranged from −13°C in December to 4°C in April. Surface water temperatures generally ranged from 4 to 5°C.

Figure 1
Kachemak Bay, Alaska, indicating bottom substrates (Driskell and Lees 1977, SAI 1979) in areas where birds were collected (Key: BC = boulders and cobbles; SD = shell debris; MS = muddy sand; MF = mudflats)



5. Methods

5.1. Field methods

We collected birds for stomach samples from a 5-m open skiff during monthly field trips of 3–5 days duration from November 1977 through April 1978. We also recorded general observations of the birds' distribution and behaviour. We worked on the north side of the bay and generally stayed on the lee side of Homer Spit during adverse or threatening weather. Birds were collected only if they were sitting on the water. We often saw Oldsquaws actively diving (and presumably feeding) in the shallow inner bay before collecting them, but we never observed the generally wary scoters do so. Immediately after collection we injected the stomachs of specimens with 10% buffered Formalin to arrest digestion (van Koersveld 1950). Specimens were then frozen until laboratory processing.

We collected 28 Oldsquaws, including 5 each month from November through February in the inner bay, 6 in March in the outer bay, and 1 each in the inner and outer bays in April. We collected 39 White-winged Scoters, as follows: 1 in November and 2 in December in the inner bay, and 14 in January and 5 each in February, March, and April in the outer bay. All birds were collected within a few kilometres of the north shore of the bay at depths ranging from about 2 to 20 m (mean lower–low water).

5.2. Laboratory methods

In the laboratory we recorded body weight and sex of the specimens and removed the esophagus, proventriculus, and gizzard intact. The stomach was carefully cut open, the contents drained of excess moisture, weighed to the nearest 0.1 g, and the volume measured to the nearest millilitre by water displacement. We then counted and identified the prey items to the lowest possible taxon and visually estimated their volume as a percent of the total. The greatest length of whole specimens was measured to the nearest millimetre. All data were recorded on a standardized form.

5.3. Methods of data analysis

We used three basic parameters to describe prey taxa in the stomach samples: aggregate percent volume (*cf.* Martin *et al.* 1946, Swanson *et al.* 1974), aggregate percent numbers, and percent frequency of occurrence. We calculated these three parameters both for species and certain higher taxa, for individual months, and for samples pooled for the entire study. Details are reported in an administrative report (Sanger and Jones 1982) and summarized in sections 6 and 7.

Differential digestion rates of hard- and soft-bodied prey may distort their original relative volumes; percent numbers can make an abundant small prey seem more

important than a sparse larger one, and percent frequency of occurrence ignores numbers and volume. Pinkas *et al.* (1971) attempted to overcome these shortcomings by combining the three values into an Index of Relative Importance (IRI), which we use here. The IRI is defined as:

IRI = $\%FO\ (\%V + \%N)$, where
$\%FO$ = % frequency of occurrence of a prey taxon in a sample of n birds.
$\%V$ = % aggregate volume of a prey taxon in the combined volume of all taxa in the stomachs of the sample of n birds.
$\%N$ = % aggregate numbers of a prey taxon in the combined numbers of all taxa in the stomachs of the sample of n birds.

We characterized the feeding habitats of the birds by comparing substrate types (Fig. 1) at their collection sites with what is known about their feeding behaviour and the habitats of their prey.

As far as possible, common and scientific names of molluscs discussed below are from Abbott (1974), those of shrimps are from Butler (1980), and those of fishes are from Robins *et al.* (1980).

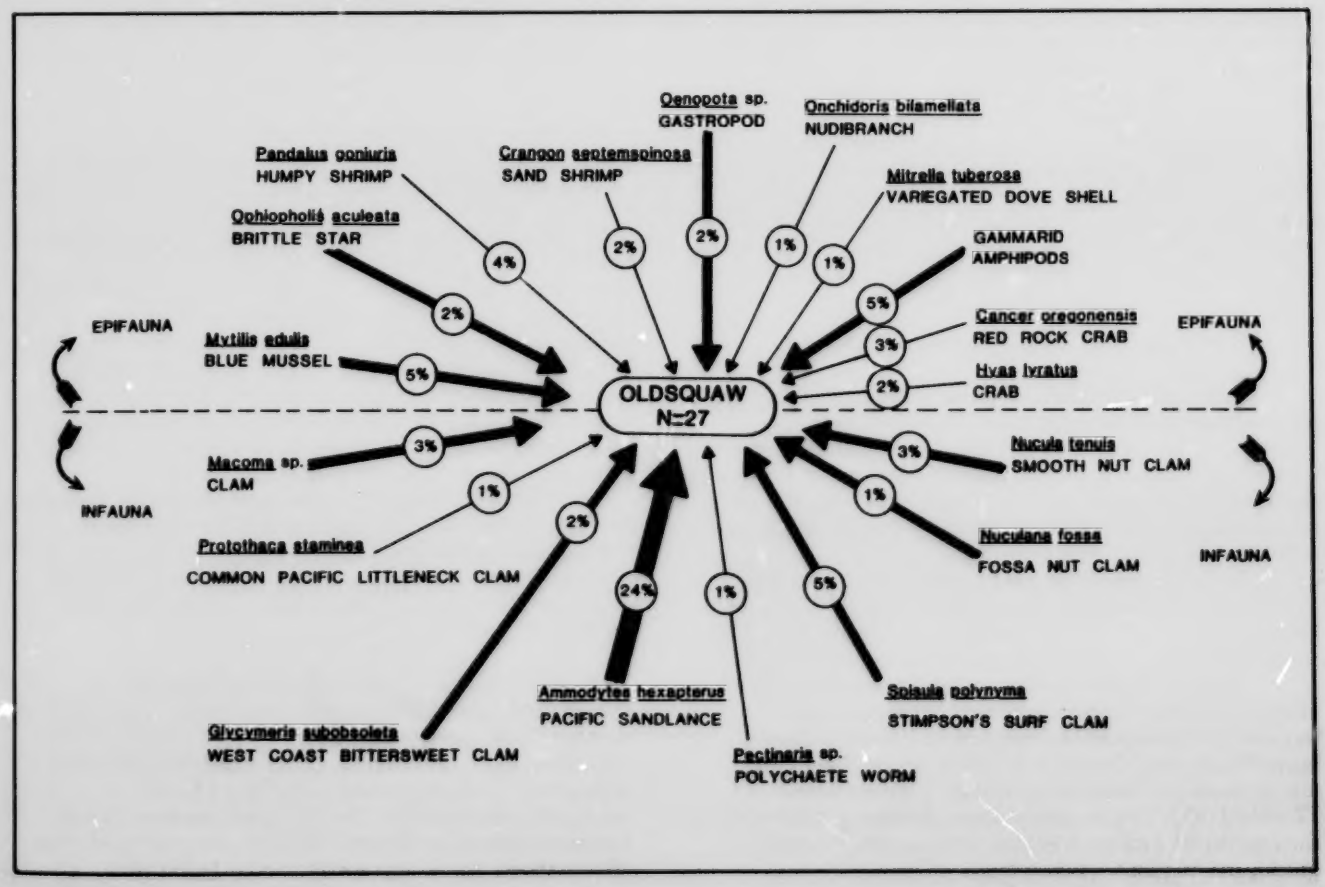
6. Oldsquaw feeding ecology in Kachemak Bay

6.1. Diet of Oldsquaws

Twenty-seven of 28 birds had identifiable prey in their stomachs; the remaining bird contained only unidentified remains. Oldsquaws ate several higher taxa of prey. These included 1 foraminiferan, 9 polychaetes, 14 gastropods, 12 bivalves, 17 crustaceans (including 1 each of a barnacle, mysid, cumacean, and isopod; and at least 8 gammarid amphipods, 3 shrimps, and 2 crabs), 1 ectoproct, 3 echinoderms (including 2 brittle stars and 1 sea urchin), and 2 fish. The most important higher taxa and their IRI values were bivalves, 3170; crustaceans, 1393; fish, 1168; gastropods, 523; and polychaetes, 321.

With a minimum total of 61 prey species (Sanger and Jones 1982), Oldsquaws had an extremely diverse diet. A sink food web (Cohen 1978) illustrates the relative importance of the 18 most important species of prey, based on their IRI values (Fig. 2). Only those prey with both an IRI of at least 10 and which constituted at least 1% of the volume are included. The dominating importance of Pacific sandlance (*Ammodytes hexapterus*) is readily seen.

Figure 2
Food web for 27 Oldsquaws wintering on Kachemak Bay, showing primary kinds of prey and their respective % of total prey volume. (Only prey with an IRI of 10 or more and which constituted at least 1% of the volume are included. Arrow sizes based on IRI value of prey, as follows: small = 10–99; medium = 100–999; large = 1000–9999)



The most important taxa overall and their IRI values were Pacific sandlance, 1059; Stimpson's surf clam (*Spisula polynyma*), 935; blue mussel, 892; smooth nut clam (*Nucula tenuis*), 215; west coast bittersweet (clam) (*Glycymeris subobsoleta*), 195; fossa nut clam (*Nuculana fossa*), 106; and the turrid gastropod *Oenopota* sp., 114. Except for sandlance, and perhaps the Stimpson's surf clam and blue mussel, it is difficult to say if these species were truly more important than many of the others. The species composition in the diet was radically different from month to month, and some higher taxa like gammarid amphipods (383) were collectively more important than most species of bivalves. Infauna made up 40% of the total volume of the prey, and it is assumed that Oldsquaws captured sandlance when they were buried in the sand (Meyer *et al.* 1979).

6.1.1. *Monthly changes in prey importance* — Small sample sizes limit statistical evaluation of monthly changes in the importance of various prey, but general trends were indicated. Fish, mostly sandlance, were present in the Oldsquaws' diet each month except February and April. Crustaceans were moderately important throughout the study, but no one species nor higher taxon was consistently important.

Other prey taxa fluctuated in their importance in no apparent pattern. A shrimp (*Spirontocaris spina*), mysids, and echinoderms (brittle stars and sea urchins) occurred only in the diet of birds collected in the outer bay during March. Bivalves and other prey displayed no monthly trends.

6.1.2. *Prey size* — Lengths of 34 prey species of Oldsquaws (Sanger and Jones 1982) ranged from 1-mm variegated lacunas (periwinkle) (*Lacuna variegata*), *Macoma* sp. clams, and blue mussels, to sandlance of 115 mm; 95% of the prey were less than 10 mm, and only 2% were over 19 mm. The mean length of 1079 measurable prey was 6.8 mm (SE = 0.33) Most of the measurable prey were gastropods (N = 84) and bivalves (N = 928).

Most bivalves were less than 6 mm, but data for *Macoma* sp. and blue mussels suggest the presence of at least a few older animals. Abbott (1974) noted 76 mm as the maximum length attained by blue mussels, so those of less than 10 mm were clearly subadults. Stimpson's surf clams, 88% of them 2–4 mm, were all age class "0" (Feder and Paul 1981).

6.2. Feeding habitats and feeding behaviour

The kinds of bottom substrates over which the birds were collected and the species and habits of their prey suggest that the Oldsquaws taken had fed benthically on both infauna and epibenthos. We observed birds mainly in the northern inner bay over mud–sand substrates, but we occasionally saw them in the outer bay over shell debris and cobble habitats.

We often saw Oldsquaws actively diving (and presumably feeding) within pan and brash ice in the inner bay behind Homer Spit. The ice probably protected the birds by shielding them from the wind and by damping the waves.

With the exception of sandlance and various species of shrimp, the Oldsquaws' prey were sessile or weakly mobile. The birds possibly captured sandlance that were buried in the sand (Meyer *et al.* 1979), although they are known to eat free-swimming fishes (e.g. Peterson and Ellarson 1977). The preponderance of sessile animals in their diets may indicate a limited adaptation for capturing quickly moving fauna, however.

Values on the weight of food in stomachs as compared with the net weight of individual birds imply that Oldsquaws did not eat large amounts of food at any one time. These values ranged from a low of 0.2% in November and February to a high of 3.0% for a bird in March (20 g of food in a 674-g bird). Average monthly values were very low, ranging from 0.45% (SE = 0.15) in April, to 1.6% (SE = 0.32) in March. The overall average for the 28 specimens was 1.0% (SE = 0.19). Sixteen birds (57%) had values less than 1.0%, but only four (14%) had values greater than 1.5%.

7. White-winged Scoter feeding ecology in Kachemak Bay

7.1. Diet of White-winged Scoters

The stomach of one specimen in February was empty, but the remaining 38 birds (97%) had food in their stomachs (there are no prey volume data for one specimen). Two other specimens collected in February 1977 as part of another project on the south side of the outer bay both contained food. Overall IRI values show that the most important major prey taxa by far were bivalves (6112) and gastropods (1510). Polychaete worms and crustaceans (16 each), and echinoderms (6) were of minor importance. White-winged Scoters had a fairly diverse diet, eating a minimum of 22 species of prey (Sanger and Jones 1982).

A sink food web of the seven main prey species (Fig. 3) illustrates the importance of blue mussels (IRI 1158) and the common Pacific littleneck (clam) (*Protothaca staminea*) (IRI 1996). These species made up 31 and 32%, respectively, of the aggregate prey volume; this contrasts to their low importance to Oldsquaws. A gastropod, the puppet margarite (*Margarites pupillus*) (IRI 151), was relatively important compared with the remaining prey, none of which had an IRI value higher than 60. Volumes of the main epifaunal and infaunal prey were about equal in the scoters' diet (Fig. 3).

7.1.1. *Monthly changes in prey importance* — Monthly sample sizes were small, but some dietary changes in birds collected were apparent. Bivalves, in particular, and gastropods were consistently important in the scoters' diet. Other major taxa were of minor importance and occurred sporadically. The blue mussel was the only prey in three birds collected in the inner bay in November and December. The common Pacific littleneck clam was consistently important to scoters collected in the outer bay from January through April, but other prey taxa were sporadic in the scoters' diet.

The two birds collected on the south side of the outer bay in February 1977 had eaten mostly the clam *Astarte rollandi* and the west coast bittersweet. Differences in prey species compared with the north side of the bay may have reflected differences in prey availability rather than prey selection.

7.1.2. *Prey size* — Lengths of 14 prey species of scoters (Sanger and Jones 1982) ranged from common northern admetes (gastropod) (*Admete couthouyi*) of 4 mm to a *Nephtys* polychaete worm of 105 mm. Lengths of 103 measurable prey pooled from all stomachs averaged 13.6 mm (SE = 1.42). Some 90% of the prey were less than 20 mm, but the occasional presence of bivalves and gastropods over 40 mm shows that scoters sometimes ate larger prey.

7.2 Feeding habitats and feeding behaviour

The kinds of bottom substrates over which the birds were collected and the species and habits of their prey suggest that the birds taken fed exclusively in benthic habitats, usually in areas with shell debris and boulder–cobble substrates, but occasionally in sand and mud. White-winged Scoters occurred relatively infrequently in the inner bay over sand–mud substrates (Erikson 1977 and this study), and the three we collected there contained only blue mussels. Thus, the scoters may have captured prey such as *Macoma* clams and arctic naticas (gastropod) (*Natica clausa*), animals typical of sand and mud (Keen and Coan 1974), in pockets of such substrates amid the shell debris and cobbles in the outer bay (Dennis Lees, pers. commun.).

The fairly wide range in prey sizes indicates that, although scoters are able to selectively eat molluscs as large as 70 mm, they probably sieve through the substrate to locate smaller prey; about half their prey were infauna. It is unlikely that much light reaches the scoters' feeding habitats, which suggests that the birds locate their food by probing the substrate with their bill and tongue, which are richly supplied with tactile nerve endings (Welty 1962:90).

The weights of food in stomachs as compared with weights of individual birds suggest that, like the Oldsquaws, White-winged Scoters ate only small amounts of food at any one time. These values ranged from zero (empty stomach) in February 1978 to a high of 4.0% for one bird each in February and March. The latter bird, weighing 1911 g, had 78 g of food in its stomach, the maximum observed. Average values from November through April ranged from 2% to 2.6%, and the overall mean for the 39 birds was 2.2% (SE = 0.16). Only five birds (13%) had values less than 1%; this, considered with the fact that only one bird had an empty stomach, suggests that the birds were consistently able to find food.

8. Comparisons between diets of Oldsquaws and White-winged Scoters

The Oldsquaws and White-winged Scoters we collected ate substantially different species of prey (*cf.* Figs. 2 and 3). We encountered Oldsquaws primarily in the inner bay over substrates of sand and mud, and most of the White-winged Scoters we saw were in the outer bay over substrates of cobbles and shell debris.

Figure 3
Food web for 37 White-winged Scoters wintering on Kachemak Bay, showing primary prey species and their respective % of total prey volume. (Only prey with an IRI of 10 or more and which constituted at least 1% of the volume are included. Arrow sizes based on IRI value of prey, as follows: small = 10–99; medium = 100–999; large = 1000–9999)

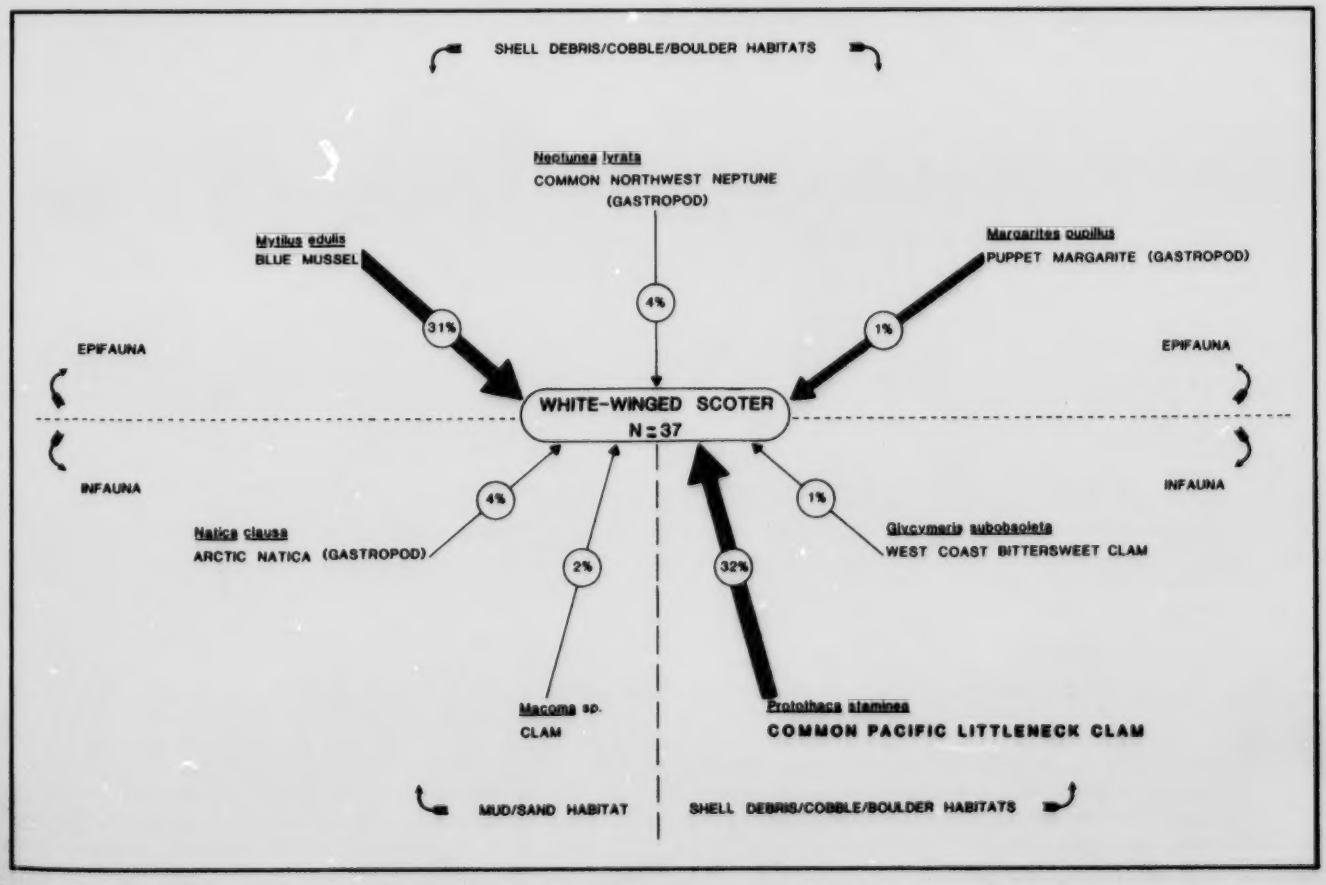
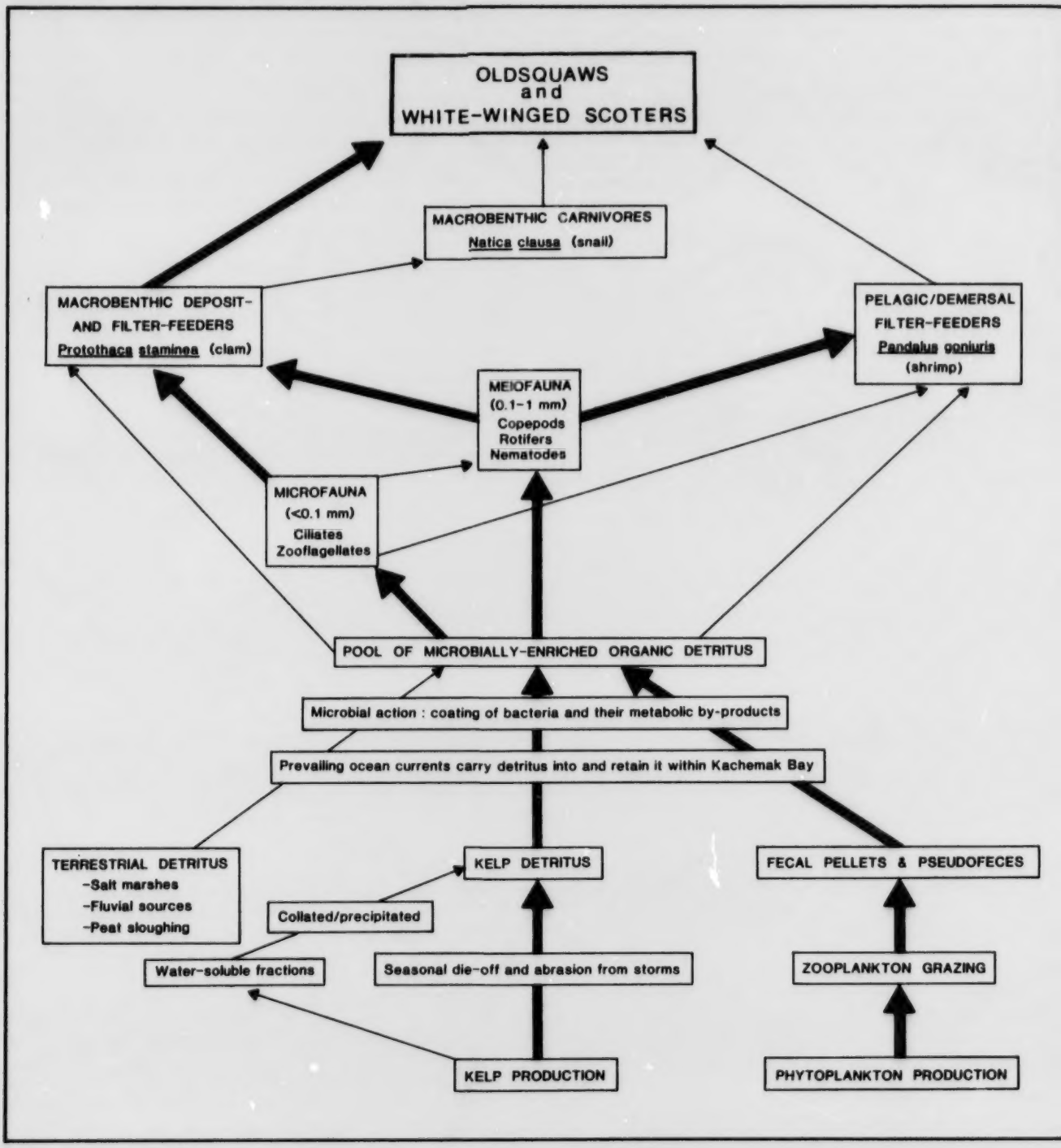


Figure 4
Hypothesized trophic relationships and environmental processes in the ecosystem of waterfowl wintering on Kachemak Bay. (Representative prey species indicated where possible, and large and small arrows show respective major and minor energy pathways)



Both sea ducks ate blue mussels and common Pacific littleneck clams. Although these species were major prey of scoters, they were of only minor importance to Oldsquaws. Moreover, lengths of these prey were markedly different for the two birds. Blue mussels (n = 432) from the Oldsquaws were all less than 10 mm, whereas the three from the scoters were 50–69 mm. Similarly, the 19 common littleneck clams from the Oldsquaws were less than 10 mm, whereas the 4 from the scoters ranged from 10 to 49 mm. Differences in average lengths of all prey (*cf.* sections 6.1.2. and 7.1.2.) were highly significant between the two species (99% level, as measured by a t-test of the differences between two means).

9. Trophic levels between primary production and seaducks

The classical view of primary production in the sea emphasizes the role of phytoplankton in the water column (e.g. Sieburth and Jensen 1970, Strickland 1970, Steele 1974). Larrance and Chester (in press) believe that the production of fecal pellets from zooplankton grazing on phytoplankton is the main source of organic detritus reaching the floor of outer Kachemak Bay in spring and summer.

However, recent work elsewhere (Tenore 1977, Mills 1975, Sieburth and Jensen 1970, Strickland 1970) has shown that organic detritus from other sources may also play a major role in driving coastal marine ecosystems. Lees and Driskell (1981) contend that abrasion of laminarian and fucoid kelps around the southern end of the Kenai Peninsula and in Kachemak Bay provides the major source of detritus. Water soluble organic fractions from kelp may also contribute to detritus (Lees and Driskell 1981, Sieburth 1968, Sieburth and Jensen 1970). Other sources of organic detritus in the bay are of terrestrial origin from streams, from salt marshes bordering the bay (J. H. Crow, unpubl. data), and from peat and coal sloughing directly into the bay along the north shore (M.P. Wennekens, pers. commun.).

Most prey of Oldsquaws and White-winged Scoters are deposit or filter feeders (Lees and Driskell 1981, Feder and Paul 1981), and, as such, they use organic detritus and its bacterial coating and associated microfauna (Tenore 1977) for food. Thus, the birds' food supply is closely linked to the existence and production of organic detritus. Although the relative importance in the ecosystem of Kachemak Bay of phytoplankton productivity and organic detritus from its various sources is unclear, lower trophic levels of the food web could be similar to detrital food chains in other coastal marine ecosystems (Tenore 1977); i.e. organic detritus — microbenthos (animals <0.1 mm) — meiobenthos (animals 0.1–1.0 mm) — macrobenthos (animals >1 mm) — fish.

In Kachemak Bay, starfish are apex predators along with fish and birds (Lees and Driskell 1981). However, the exact trophic level(s) at which apex predators feed is unknown because the nature of the microbenthos and meiobenthos are virtually unknown (Robert Griffiths, pers. commun.). The filter- and deposit-feeding prey of the birds could feed on any of these animals, and also directly ingest the bacterially-enriched detritus. Thus, depending on which of these links are present in the food web of Kachemak Bay, Oldsquaws and scoters function as first- to fourth-order carnivores. For example, when Oldsquaws eat humpy shrimp (*Pandalus goniuris*) that eat detritus, the Oldsquaws are first-order carnivores. When White-winged Scoters eat *Natica clausa* snails, that eat clams, that eat meiofauna, that eat microfauna, that eat detritus, the scoters are fourth-order carnivores.

With these points in mind, the possible environmental processes and trophic relationships in the ecosystem of birds wintering in Kachemak Bay (Fig. 4) may be summarized as follows:

1. Stocks of kelp in Kachemak Bay and around the southern end of the Kenai Peninsula grow intensively in spring and summer, when phytoplankton in the area also blooms intensively.

2. Fecal pellets from zooplankton and the abrasion and seasonal die-off of kelp both produce organic detritus.

3. Currents carry the kelp detritus from the southern end of the Kenai Peninsula into Kachemak Bay.

4. Bacteria colonize the detritus at some point.

5. The microbially-enriched detritus supports a rich community of deposit- and filter-feeding demersal and benthic fauna, probably by means of one or two trophic links (micro- and meiofauna).

6. The deposit- and filter-feeding animals, in turn, support marine birds and other apex predators.

10. General discussion

Oldsquaws and scoters were collected in water depths between 2 and 20 m. We do not know precisely the depths at which the birds fed, but it is likely that White-winged Scoters collected in the outer bay fed mostly at depths shallower than those studied by Feder and Paul (1981) (*ca.* 29 m) and by Driskell and Lees (1977) (*ca.* 12–65 m), and deeper than the intertidal areas studied by Lees and Driskell (1981). Feeding depths of Oldsquaws collected in the inner bay likely overlapped the 1.5–11.3-m depths surveyed by Lees and Driskell (1981).

The presence of blue mussels, an intertidal species, in both Oldsquaws and White-winged Scoters indicates that both ducks fed at least part of the time over intertidal areas at high tide, whereas the absence of the horse mussel (*Modiolus modiolus*), an exclusively subtidal species, from their diets suggests that they may not have foraged over rocky areas when they fed subtidally. Horse mussels are abundant in the outer bay off Homer Spit, and off Bluff Point (Lees and Driskell 1981), where we collected many of the scoters. Mussels from Bluff Point, however, range in length from 75 to 150 mm (Driskell and Lees 1977), which may have been too large for the scoters.

Oldsquaws and White-winged Scoters from Kachemak Bay ate the same general taxa of prey reported from other areas (e.g. Vermeer and Bourne, this volume, Stott and Olson 1973, Nilsson 1972, Madsen 1954, Cottam 1939); both species eat mostly bivalves, gastropods, and crustaceans. However, knowledge of the availability of the birds' prey species relative to the availability of other potential prey in Kachemak Bay is sketchy. There is some similarity between the Oldsquaws' diet and benthic fauna reported from surveys in the inner bay (Lees and Driskell 1981). Animals present in the non-quantitative surveys that were also present in the Oldsquaws' diet included turrid gastropods (*Oenopota* sp.), blue mussels, *Nuculana* and *Macoma* clams, and sandlance. Dominant benthic species on rocky substrates between 4 and 16 m during SCUBA diving surveys along the north shore of the outer bay (Lees and Driskell 1981) included the horse mussel, matting polychaete *Potamilla*, butter clam *Saxidomus* sp., green sea

urchin (*Strongylocentrotus droebachiensis*), and common northwest neptune (gastropod) (*Neptunea lyrata*). Of these, only the neptune was moderately important to White-winged Scoters, and the green sea urchin was of minor importance; the others were absent from the scoters' diet.

The general contrast between the birds' diets and the fauna identified from benthic surveys suggests that there may be differences between the kinds of animals present in the birds' feeding habitats and the areas surveyed. It is also possible that the surveys missed components of the birds' diets, and that the birds selected prey in different proportions to their occurrence in nature. In view of the size range of horse mussels off of Homer Spit (15–130 mm, Lees and Driskell 1981), the absence of smaller individuals in the diet of the scoters is puzzling.

Amounts of food in the birds ranged up to 3–4% of their net body weight; similar data on other waterfowl appear to be lacking. Despite this seeming paucity of food, however, body weights reflected a healthy condition of the birds (Sanger and Jones 1982). Also, rapid digestion rates (van Koersveld 1950) and frequent small feedings are indicated.

11. Acknowledgements

A. Fukuyama, A. DeGange, R. Gill, M. Petersen, and D. Nysewander, US Fish and Wildlife Service, assisted with field work. We thank L. Flagg, D. Hardy, and C. Larson, Alaska Department of Fish and Game, for hospitality and logistics support in Homer.

Stomach contents were processed and identified by D. Wiswar (scoters) and A. Fukuyama (Oldsquaws). G. Mueller and staff, Marine Sorting Center, University of Alaska, were particularly helpful with identifications. They and other specialists who helped were: J. Blackburn, fishes; K. Coyle, crustaceans; W. Driskell, gastropods; N. Foster, gastropods and pelycypods; K. Frost and L. Lowry, fish otoliths; H. Jones, polychaetes; H. Kajimura, fish bones; G. McDonald, nudibranch gastropods; and, G. Mueller, bryozoans, crustaceans, ophiuroids, and polychaetes.

Discussions and correspondence with P. Arneson, D. Erikson, R. Griffiths, and D. Lees on Kachemak Bay and its biota were very helpful. D. Amos, D. Wiswar, and T. Martinson assisted with data analyses and/or graphics. D. Amos, A. Fukuyama, D. Derksen, L. Krasnow, D. Lees, C. Lensink, M. Petersen, S. Peterson, P. Springer, and D. Wiswar commented on various drafts of this paper.

This study was supported by the Bureau of Land Management (BLM) through interagency agreement with the National Oceanic and Atmospheric Administration (NOAA), under which a multi-year program responding to needs of petroleum development of the Alaskan continental shelf is managed by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) Office, Juneau.

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The White-winged Scoter diet in British Columbia waters: resource partitioning with other scoters

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1. Abstract

The diet of White-winged Scoters (*Melanitta fusca deglandi*) was examined in British Columbia marine waters. Scoters are opportunistic and forage in various intertidal and subtidal zones over different substrates. At least 20 bivalve and 20 snail species were encountered as prey, which varied among regions. Of the bivalves, six clam species predominated, but blue mussels (*Mytilus edulis*) were important at one location. Of the snails, only *Batillaria attramentaria* contributed significantly to the scoter's food biomass. Barnacles were the most important crustacean food.

The distribution and food of White-winged Scoters were compared with those of Black (*Melanitta nigra*) and Surf scoters (*Melanitta perspicillata*). All three species are found over sand–mud and cobble substrates. White-winged Scoters are also abundant over gravel beds and Surf Scoters over rocky substrates. Surf Scoters outnumbered other scoters along the steep rock walls of fiords.

White-winged Scoters ate more clams and snails than did the other two scoter species, whose diets were composed mainly of mussels. Where scoters foraged over or near clam beds, the Surf Scoter partly switched from mussels to Manila clams (*Tapes philippinarum*) while the Black Scoter remained with its mussel staple. The implications of those prey preferences with respect to the scoters micro-feeding habitat are discussed.

White-winged Scoters selected larger clams and blue mussels than Surf and Black scoters. Black Scoters ate similarly sized mussels as did Surf Scoters, which suggests interspecific competition for that resource.

2. Résumé

Nous avons étudié le régime des Macreuses à ailes blanches (*Melanitta fusca deglandi*) dans les eaux salées de la Colombie-Britannique. Les macreuses sont opportunistes et puisent leur nourriture dans différentes zones intertidales et subtidales au-dessus de différents substrats. Parmi leurs proies, nous avons dénombré au moins 20 espèces de bivalves et 20 espèces d'escargots qui variaient selon les régions. Parmi les bivalves, six espèces prédominaient, mais la moule bleue (*Mytilus edulis*) était importante en un endroit. Parmi les escargots, seul le *Batillaria atramentaria* contribuait de façon significative à la biomasse alimentaire des macreuses. La balane était le crustacé le plus consommé.

Nous avons comparé la répartition et l'alimentation de la Macreuse à ailes blanches à celles de la Macreuse à bec jaune (*M. nigra*) et de la Macreuse à front blanc (*M. perspicillata*). Nous trouvons les trois espèces sur des substrats de sable, de boue et de cailloux roulés. Les Macreuses à ailes blanches sont aussi abondantes sur les lits de gravier et les Macreuses à front blanc, sur des substrats rocheux. Ces dernières étaient d'ailleurs plus nombreuses que les autres macreuses le long des falaises des fiords.

Les Macreuses à ailes blanches mangeaient plus de bivalves et d'escargots que les deux autres espèces, dont le régime se composait principalement de moules. Quand les macreuses pêchaient au-dessus ou près de lits de bivalves, la Macreuse à front blanc passait à l'occasion des moules aux tapes japonais (*Tapes philippinarum*) tandis que la Macreuse à bec jaune restait fidèle à son régime de moules. Nous discutons des répercussions de ces préférences pour certaines proies sur l'habitat micro-alimentaire des macreuses.

Les Macreuses à ailes blanches choisissaient de plus gros bivalves et moules bleues que les Macreuses à front blanc et les Macreuses à bec jaune. Les Macreuses à bec jaune mangeaient des moules de même grosseur que les Macreuses à front blanc, ce qui laisse croire à une concurrence interspécifique pour cette ressource.

3. Introduction

The White-winged Scoter has an almost circumpolar distribution in the northern hemisphere. There are three main races, of which the American one, *Melanitta fusca deglandi*, breeds in northwestern Canada and Alaska and winters on the Atlantic and Pacific coasts of North America (Bellrose 1976).

On the North American Atlantic coast White-winged Scoters feed chiefly on bivalves that include blue mussels (*Mytilus edulis*), mussels (*Yoldia* sp.), Atlantic razor clams (*Siliqua costata*), arctic wedge clams (*Mesodesma arctatum*), northern quahogs (*Mercenaria mercenaria*), and scallops (*Argopecten irradians*) (Cottam 1939, McGilvrey 1967, Cronan and Halla 1968, Stott and Olson 1973). Gastropods can be important inasmuch as Atlantic dogwinkles (*Nucella lapillus*) were observed to be a chief White-winged Scoter food item in Maine (McGilvrey 1967).

Important White-winged Scoter foods along the North American Pacific coast include rock clams (*Macoma inquinata*) in California (Grosz and Yocom 1972), Manila clams (*Tapes philippinarum*, also known as *T. japonica* by some authors) and common Pacific littlenecks (*Protothaca staminea*) in Washington (Glude 1967, Hirsch 1980), olympic oysters (*Ostrea lurida*) over planted oyster beds in Washington (Cottam 1939), and basket cockles (*Clinocardium nuttalli*) and snails (*Batillaria attramentaria*, formerly known as *B. zonalis*)

on the Fraser Delta in British Columbia (Vermeer and Levings 1977).

The objectives of this study were to determine prey variability in White-winged Scoters and compare their diets and distribution with Black Scoters (*Melanitta nigra*) and Surf Scoters (*Melanitta perspicillata*) in British Columbia waters.

4. Methods

White-winged Scoters were collected with a shotgun from a boat in January and February (north coast of Denman Island, 1967–1968; Fraser Delta, 1974, 1976; south coast of Saltspring Island, 1977), March and April (south coast of Saltspring Island, 1978; north coast of Denman Island, 1968), July and August (Fraser Delta, 1974), and October and November (south coast of Saltspring Island, 1978; north coast of Denman Island, 1968; Cumshewa Inlet, 1980) (Fig. 1). The food habits of White-winged Scoters on the Fraser Delta have been reported previously by Vermeer and Levings (1977), but the data were consolidated for the seasons. The collection areas in the present study represent different coastal habitats. Waters at northern Denman Island cover a sand-gravel-mud-shell substrate; the Fraser Delta has extensive mud flats; southern Saltspring Island is a representative of the Gulf Islands with a rocky substrate, interspersed with sand-shell-mud; and Cumshewa Inlet on the east coast of Moresby Island has primarily a cobble and gravel substrate. These areas have a maximum tidal range of 5 m, except Saltspring Island which has a range of 3.7 m. Stomachs and esophagi of the White-winged Scoters were dissected within 1 h of collection and the food contents stored in 10% Formalin. Food contents of stomachs and esophagi were consolidated as most prey of White-winged Scoters in marine waters have either hard shells or exoskeletons. The presence of soft foods could bias the data if consumed with hard foods that resist digestion.

Figure 1
Location of study areas in British Columbia waters

Surveys of bird numbers were made from a fishing vessel along the east coast of the Queen Charlotte Islands in October 1976 and from a hydrographic vessel along the coast of the Strait of Georgia and adjacent fiords in March and November 1977. Bi-monthly surveys were conducted from a small boat 20–100 m from the shores of Saanich Peninsula and nearby Gulf Islands in southern Georgia Strait from September 1977 to May 1978. Observations were made through 8-by-30 binoculars.

Distribution and abundance of bivalves and gastropods in intertidal and subtidal areas has been gathered since 1930 by several researchers of the Pacific Biological Station, Nanaimo in conjunction with regular sampling and dragging programs in the littoral waters of British Columbia (Bernard 1970).

Statistical significance was determined with the Fisher Exact Test for proportions (Zar 1974). The principal references used for scientific names of molluscs and crustaceans were Abbott (1974) and Kozloff (1976), respectively.

5. Results and discussion

5.1. Food of White-winged Scoters

The three main food categories eaten by White-winged Scoters were bivalves, gastropods, and crustaceans (Fig. 2, Table 1). Bivalves were a principal prey at all locations, and gastropods formed a substantial portion of the scoters' diet on the Fraser Delta. Crustaceans were important prey at Denman Island in both autumn and winter and on the Fraser Delta in summer.

5.1.1. *Bivalves* — At least 20 bivalve species were observed in the White-winged Scoter diet (Table 1), but only seven were taken in substantial amounts (Fig. 2). Prey species varied among regions and seasons. Important items were basket cockles on the Fraser Delta in winter and summer, and at Saltspring Island in autumn; common Pacific littlenecks and Manila clams, the latter a species introduced from Japan, at Denman Island in autumn, winter, and spring; Manila clams at the Fraser Delta in winter; blue mussels at Cumshewa Inlet and Saltspring Island in autumn; butter clams (*Saxidomus giganteus*) and *Macoma* sp. at Saltspring Island in winter; and *Acila castrensis* and basket cockles at Saltspring Island in autumn. A major seasonal

Table 1
Percentage occurrence and wet weight of prey items and grit in White-winged Scoters at four British Columbia locations

	Fraser Delta				Saltspring Island				Denman Island						Cumshewa Inlet	
	Winter 1974,1976		Summer 1974		Autumn 1978		Winter 1977–1978		Autumn 1967,1968		Winter 1968		Spring 1968		Autumn 1980	
Prey items	Occ.	Wt., g	Occ.	Wt., g	Occ.	Wt., g	Occ.	Wt., g	Occ.	Wt., g	Occ.	Wt., g	Occ.	Wt., g	Occ.	Wt., g
Bivalves	71.4	45.8	93.8	39.6	94.7	88.1	100.0	100.0	82.1	62.5	94.1	59.8	100.0	79.6	91.3	58.4
Protothaca staminea	35.7	7.7							51.8	27.2	52.9	15.8	60.0	37.5	4.3	3.6
Tapes philippinarum	21.4	16.7							46.4	29.0	79.4	40.0	62.9	27.7		
Clinocardium nuttalli	35.7	17.6	25.0	31.8	63.2	20.8			12.5	1.4						
Clinocardium fucanum					5.3	6.4										
Mytilus edulis			18.8	3.1	15.8	18.4			25.0	4.7	32.3	3.5	31.4	6.4	87.0	54.4
Mya arenaria	14.3	3.5														
Macoma nasuta													5.7	2.9		
Macoma sp.			31.3	2.0	31.6	4.7	66.7	43.3								
Saxidomus giganteus					21.1	7.6	88.9	56.2			2.9	0.1	11.4	4.9	4.3	0.4
Acila castrensis					31.6	21.6										
Pandora filosa					21.1	0.7			2.0	0.2						
Transenella tantilla					21.1	0.5										
Compsomyax subdiaphna					10.5	4.7										
Lyonsia californica					5.3	0.2										
Nucula tenuis					5.3	0.2										
Nuculana minuta					5.3	0.2										
Liocyma fluctuosa					5.3	0.2										
Cyclocardia ventricosa					5.3	0.2										
Axinopsis serricata					5.3	0.2										
Gari californica											2.9	0.4				
Tresus capax							11.1	0.5					2.9	0.2		
Unident. bivalve fragments	7.1	0.3	56.3	2.7	10.5	1.5										
Gastropods	85.7	38.2	43.8	8.6	57.9	6.0			23.2	4.8	41.2	1.3	48.6	9.2	43.5	20.0
Batillaria attramentaria	71.4	32.0	25.0	3.7					1.8	3.5			11.4	5.7		
Nassarius obsoletus	7.1	3.6														
Nassarius mendicus	7.1	1.0			15.8	0.4			8.9	0.7	2.9	trace	11.4	0.4	8.7	1.7
Turbonilla eschscholtzi	7.1	0.2														
Mitrella gausapata					26.3	3.0			5.4	0.4						
Margarites pupillus					5.3	2.2										
Margarites succinctus					5.3	trace										
Margarites lirulatus					5.3	trace										
Margarites helicinus															13.0	0.3
Bittium eschrichtii					5.3	trace									13.0	0.4
Bittium attenuatum					10.5	0.4							2.9	0.4		
Littorina scutulata					10.5	trace			10.7	0.1	32.3	1.3	14.3	2.6	21.7	0.3
Littorina sitkana					5.3	trace									30.4	14.8
Amphissa columbiana					5.3	trace									8.7	1.9
Tachyrhynchus lacteolus																
Olivella baetica									1.8	0.1			5.7	0.1		
Astraea gibberosa															4.3	trace
Searlesia dira															4.3	0.6
Thais (also named *Nucella*) sp.			6.3	3.7												
Unident. gastropod fragments	14.3	1.4	18.8	1.2												
Crabs and shrimps	21.4	15.0	6.3	9.8	26.3	4.4			3.6	0.1	5.9	0.4				
Telmessus cheiragonus	7.1	7.9														
Cancer productus			6.3	3.2												
Hemigrapsus nudus			6.3	6.6	21.1	4.2			3.6	0.1	5.9	0.4				
Upogebia pugettensis	14.3	7.1														
Spirontocaris prionota					5.3	0.1										
Heptacarpus brevirostris					5.3	0.1										
Barnacles																
Balanus glandula			25.0	39.7	10.5	trace			42.9	28.9	52.9	38.5	22.9	11.2	21.7	0.8
Polychaetes	7.1	0.4														
Plants	14.3	0.6	12.5	trace					7.1	0.5					4.3	0.1
Grit	14.3	trace	12.5	2.3	21.1	1.5			1.8	3.2					87.0	20.8
Number of scoters		14		16		19		9		56		34		35		23
Wet weight of food, g		746		300		615		248		1067		1118		1184		691

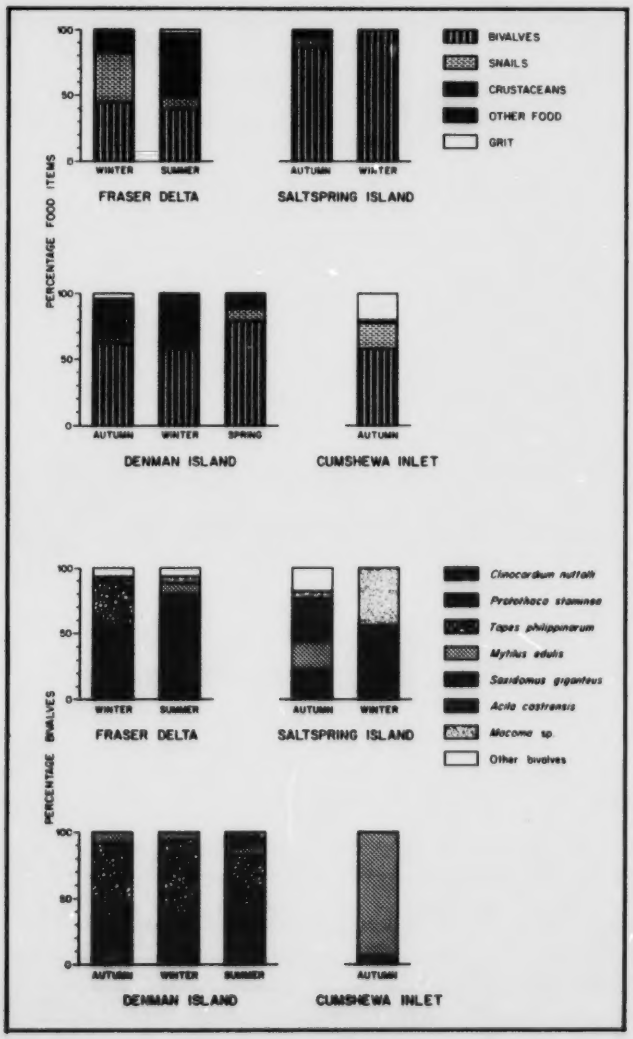
food change was observed on the Fraser Delta where scoters shifted from three principal clam species in winter to chiefly basket cockles in summer (Fig. 2). This shift may be explained in that cockles are found more frequently on the substrate surface during that season than other bivalves, where they are readily accessible to the ducks. Another seasonal food change occurred on Saltspring Island from four clam species in autumn to two species in winter (Fig. 2). No explanation can be given for the latter shift.

The bivalves eaten by White-winged Scoters reflect the abundance of prey items in the various localities. At Denman Island, Manila clams and common Pacific littlenecks are common but basket cockles are relatively scarce (Bourne, unpubl. data); in the Fraser Delta cockles are abundant but other clams are less common (Vermeer and Levings 1977); in Cumshewa Inlet clam beaches are few (Bourne, pers. observ.).

White-winged Scoters appear opportunistic in that individual stomachs contained more than one bivalve species. Of 186 bird stomachs with bivalves, 45.2% had one, 46.2% two, 7.0% three, 1.1% four, and 0.5% eight species. Bivalves eaten varied least at Cumshewa Inlet and most at Saltspring Island. At the latter location, one scoter contained eight species — basket cockles, *Compsomyax subdiaphna*, *Pandora filosa*, *Lyonsia californica*, *Nucula tenuis*, *Nuculana minuta*, *Liocyma fluctuosa*, and *Axinopsis serricata*. Scoters frequently swallowed whole bivalves. The average length of 11 blue mussels was 3.4 cm (range 1.4–4.7 cm); 60 Manila clams, 3.0 cm (range 1.4–5.3 cm); 47 common Pacific littlenecks, 3.7 cm (0.8–5.3 cm); and 6 basket cockles, 4.1 cm (range 2.1–5.4 cm).

The variety of bivalves eaten by White-winged Scoters reflects the diversity in the birds' feeding habitat. Bivalve prey occurred in different intertidal and subtidal areas as well as on different substrates (Fig. 3). Scoters fed chiefly on intertidal clams at all locations (Table 1 and Fig. 3). Some of the bivalves eaten are subtidal, e.g. *Acila castrensis*, but they were important only at Saltspring Island in autumn. Most clams bury in a silt–mud, sand, or gravel substrate, but blue mussels attach themselves to coarse gravel, boulders, solid rock, and pilings. Our results indicate that White-winged Scoters preyed primarily on species occurring on the sea-bottom rather than on rock faces. Blue mussels obtained from cobble–gravel beaches formed the main prey at Cumshewa Inlet. Much gravel occurred in scoter stomachs collected there (21%, classified as grit in Table 1).

Figure 2
Comparison of biomass of major food categories of White-winged Scoters, and of bivalves, at four British Columbia locations



5.1.2. *Gastropods* — White-winged Scoters fed on 20 gastropod species. *Batillaria attramentaria* introduced from Japan, was a particularly important food item at the Fraser Delta mudflats (Table 1). The average length of 45 *Batillaria* taken from scoters was 1.7 cm (range 0.9–2.5 cm). It is not surprising that scoters fed extensively upon that species because of its large size and abundance on the Delta mudbanks. *Batillaria* was more important as a food for White-winged Scoters in winter than summer on the Fraser Delta; this may be due to young *Batillaria*, which hatch in early summer, being larger in winter. Although gastropods were not generally important foods, their variety in the scoters' diet reflects diverse and opportunistic feeding in intertidal and subtidal zones (Fig. 4). Scoters may strip gastropods that occur on eelgrass (*Zostera marina*) and sea lettuce (*Ulva* sp.)

5.1.3. *Crustaceans* — Of the crustaceans, barnacles (*Balanus glandula*) were the most important prey of White-winged Scoters (Table 1). Barnacles appeared as a scoter food in the Fraser Delta only in summer. Barnacles may be accidentally ingested when attached to mussels, but their predominance over any other prey in many scoter meals suggests that they are selected as food. Twenty-one percent of the scoter stomachs from Denman Island contained 80 percent or more barnacles, which were often swallowed whole. Barnacle meals weighed as much as or more ($\bar{x} = 28.6$ g, $n = 26$) than did meals containing predominantly other foods such as common Pacific littlenecks and Manila clams ($\bar{x} = 26.8$ g, $n = 99$). Barnacle and mollusc shells may substitute for grit inasmuch as little gravel occurred in White-winged Scoter stomachs except at Cumshewa Inlet. Cottam (1939) also observed the use of shells as grit and marvelled at the strength and grinding power of the scoter's gizzard, stating that "as many molluscs that a man's fingers cannot break are found in it being ground and chemically disintegrated." Gizzard weights of male scoters averaged 118.4 g (range 74–175 g, $n = 10$) and those of female scoters 109.5 g (range

80–151 g, $n = 13$). Gizzards of male scoters made up 7.7% and those of female scoters, 7.9% of their respective body weights. The largest gizzard of 23 scoters measured was 10 cm across. Gizzard size apparently relates to diet. Gizzards of female White-winged Scoters in Alberta and Saskatchewan averaged 35 g during pre-laying and 19 g at the end of incubation (Brown 1981); those weights are only a fraction of gizzard weights observed in this study. White-winged Scoters chiefly eat amphipods (*Hyalella azteca*) on the breeding grounds (Brown 1981) which do not need as much grinding as barnacles and bivalves, the scoters' winter foods.

Crabs and shrimps were other common crustacean foods of White-winged Scoters (Table 1). The crab diet of scoters on the Fraser Delta consisted of helmet crabs (*Telmessus cheiragonus*), red crabs (*Cancer productus*), and purple shore crabs (*Hemigrapsus nudus*) and was the most diversified of those from the various collecting sites. Purple shore crabs were also common prey at Saltspring and Denman islands. Blue mud shrimps (*Upogebia pugettensis*) were the only shrimp found in scoters feeding on the Fraser Delta, while deep-bladed shrimp (*Spirontaris prinonota*) and stout coastal shrimp (*Heptocarpus brevirostris*) were taken as prey at Saltspring Island.

5.1.4. *Other foods* — Two White-winged Scoters (not shown in Table 1) collected at Atrevida Reef, March 1977, contained mostly Pacific herring (*Clupea harengus pallasi*) eggs. One scoter from the northern end of the Strait of Georgia (not shown in Table 1) contained mostly the chink snail (*Lacuna marmorata*) and remains of a 6-cm unidentified fish. Cottam (1939) found that White-winged Scoters occasionally eat fish.

Figure 3
Tidal-zone location and substrate of bivalve species eaten by White-winged Scoters. Rectangles indicate principal range of occurrence and horizontal lines indicate overall range of occurrence

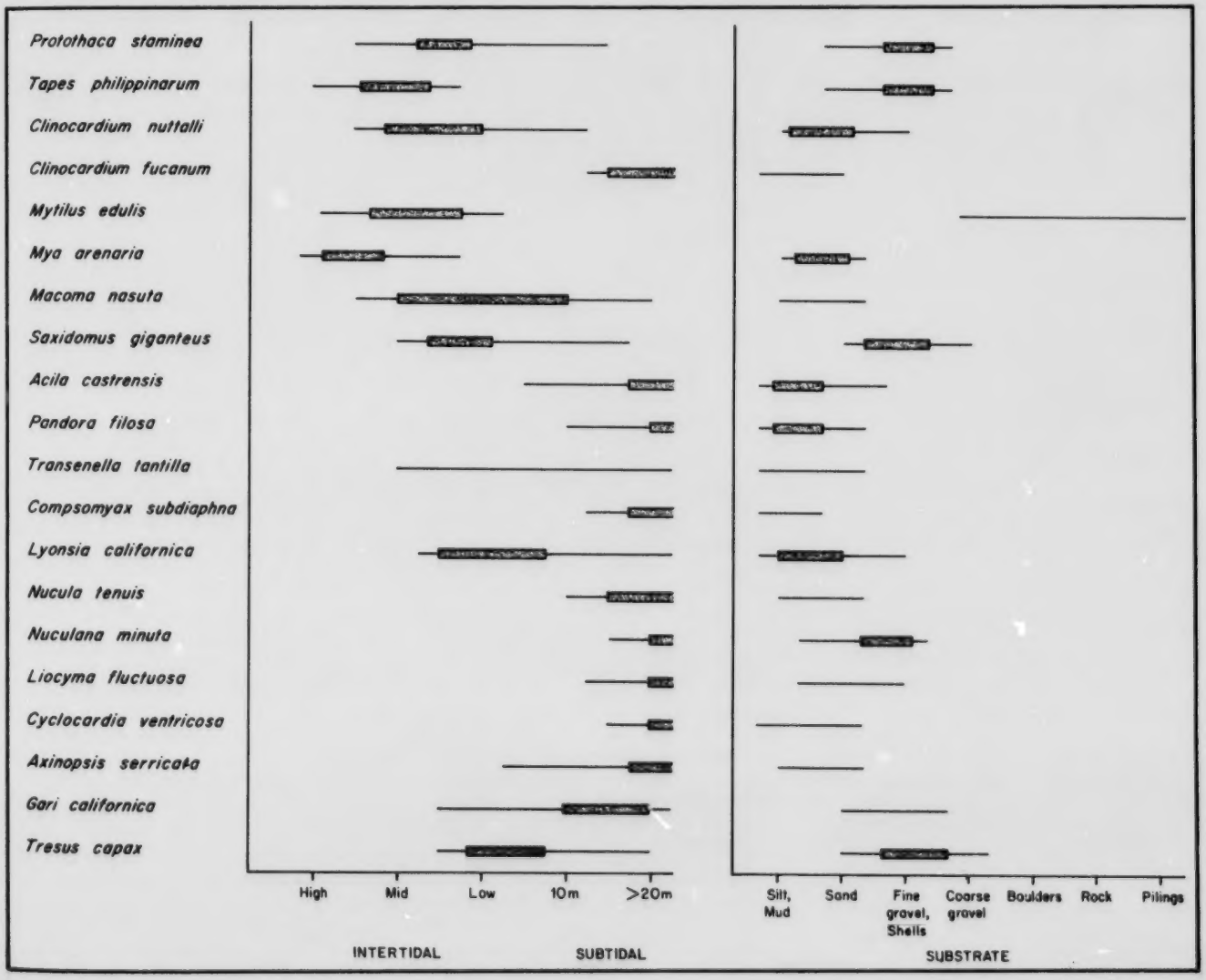
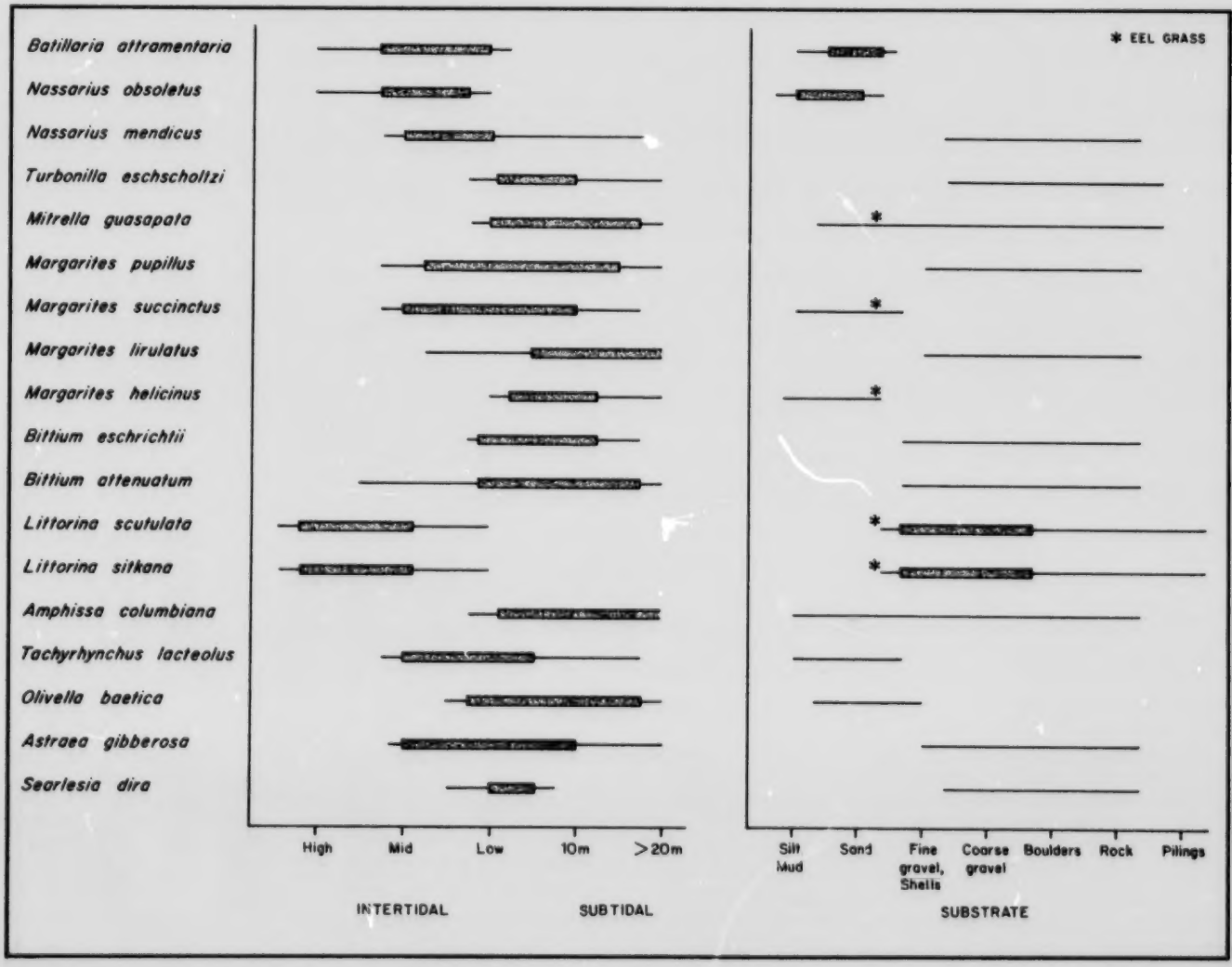


Table 2
Comparison of scoter densities as observed by boat along the Strait of Georgia coast, March and November 1977

	Number of scoters per km					
	Surf Scoter		White-winged Scoter		Black Scoter	
Location	March	November	March	November	March	November
East coast Vancouver Island	41.5	25.9	3.4	10.0	0.5	0.1
Northern Strait of Georgia	6.6	6.9	0.4	0.03	0.3	—
Mainland	46.8	24.7	0.02	0.5	—	—
Mainland fiords						
Bute Inlet	6.5	122.8	—	1.4	0.09	—
Jervis Inlet	7.9	26.5	0.01	—	—	—
Howe Sound	20.5	18.0	0.1	—	—	—
Total no. identified scoters	21 575	35 440	1182	2985	182	27
No. km shoreline surveyed	1 107	964	1107	964	1107	964
Birds/km	19.5	36.8	1.1	3.1	0.2	0.03

Figure 4
Tidal-zone location and substrate of snail species eaten by White-winged Scoters. Rectangles indicate principal range of occurrence and horizontal lines indicate overall range of occurrence



5.2. Resource partitioning with other scoters

Vermeer and Levings (1977) reported on Black, Surf and White-winged scoter diets in the Fraser Delta. The distribution and food of Surf Scoters in British Columbia have been investigated by Vermeer (1981). Bourne (unpubl. data) examined Black and Surf scoter food at Denman Island at the same time that White-winged Scoters were collected there. Information from those sources and the present data allow for comparison on the distribution and food of scoters.

5.2.1. *Macro- and micro-feeding habitats* — In British Columbia the Surf Scoter is the most numerous scoter followed by the White-winged Scoter, while the Black Scoter occurs only in small numbers (Vermeer 1981). The most apparent difference in distribution between Surf and White-winged scoters is that the former is one of the most numerous ducks in the fiords, while the latter is scarce there (Table 2, Vermeer 1981). Surf Scoters feed predominantly on blue mussels on fiord walls. White-winged Scoters are chiefly bottom feeders, and the fiords are generally too deep to allow that type of foraging. White-winged Scoters were scarce along the continuous rocky shores of the mainland coast (Table 2). They occurred in higher densities over sand–mud, gravel, and cobble substrates but were still less numerous than Surf Scoters on the east coast of Vancouver Island and in the Gulf Islands (Table 2, Fig. 5). White-winged Scoters outnumbered Surf Scoters by about one order of magnitude in autumn 1976 at northeastern Moresby Island, which includes Cumshewa Inlet, where they fed over cobble and gravel substrates.

Black Scoter populations were small compared to those of the other two scoters in British Columbia. Their numbers were most substantial in March during migration, when they occurred over sand–mud and cobble substrates between Nanaimo and Campbell River on the east coast of Vancouver Island. In March 1978 they were the main scoter species observed in kelp beds off northeastern Vancouver Island.

Differences in prey predominance in the diets of the three scoter species in the same region may define differences in their feeding habitats. Blue mussel presence reflects feeding over coarse gravel, boulders, and a rock substrate in the intertidal zone (Fig. 3). Most clams occur in a silt, mud, sand, and fine gravel substrate (Fig. 3). This suggests that at Denman Island, Black Scoters foraged in the former and White-winged Scoters in the latter habitat, whereas Surf Scoters were found over both substrates. The presence of *Acila castrensis* in White-winged Scoters and not in Surf Scoters at Saltspring Island suggests more subtidal feeding by the former. White-winged Scoters were generally seen farther from shore and in deeper waters at that location than at the other locations. Hirsch (1980) also observed that White-winged Scoters are frequently found in deeper waters than other diving ducks in areas along northern Puget Sound and the Strait of Juan de Fuca in Washington State. The greater occurrence of snails in White-winged Scoters than in the other two species indicates extensive feeding over sand–mud and fine gravel substrates and in eelgrass to which snails attach (Fig. 4). Vermeer and Levings (1977) reported that White-winged Scoters fed extensively on basket cockles (Table 3) in eelgrass beds of the lower Fraser Delta intertidal zone. The above observations show that, although the three scoter species feed in the same area, there is partitioning of feeding habitats.

5.2.2. *Diet* — The diets of the three scoters were compared when investigated at the same locations (Table 3). Bivalves formed the main diet for all three species. Black and Surf scoters fed significantly more on blue mussels than did White-winged Scoters ($P<0.05$); the main food of White-winged Scoters consisted of a variety of clams. At Denman Island, Surf and White-winged scoters fed extensively upon Manila clams whereas Black Scoters remained with their mussel staple. White-winged Scoters fed significantly more on gastropods than the Surf Scoter at Denman Island, the Fraser Delta, and Saltspring Island and than the Black Scoter on the Fraser Delta ($P<0.05$). White-winged Scoters contained significantly more barnacles than did Surf Scoters at Denman Island, and the Black Scoter ate significantly more barnacles than the Surf Scoters at the Fraser Delta ($P<0.05$). Apparently, barnacle predominance in White-winged Scoters reflects deliberate feeding on that prey, whereas the barnacles taken by Black Scoters are ingested incidentally to blue mussels. Polychaetes occurred most frequently in Black Scoters at the Fraser Delta.

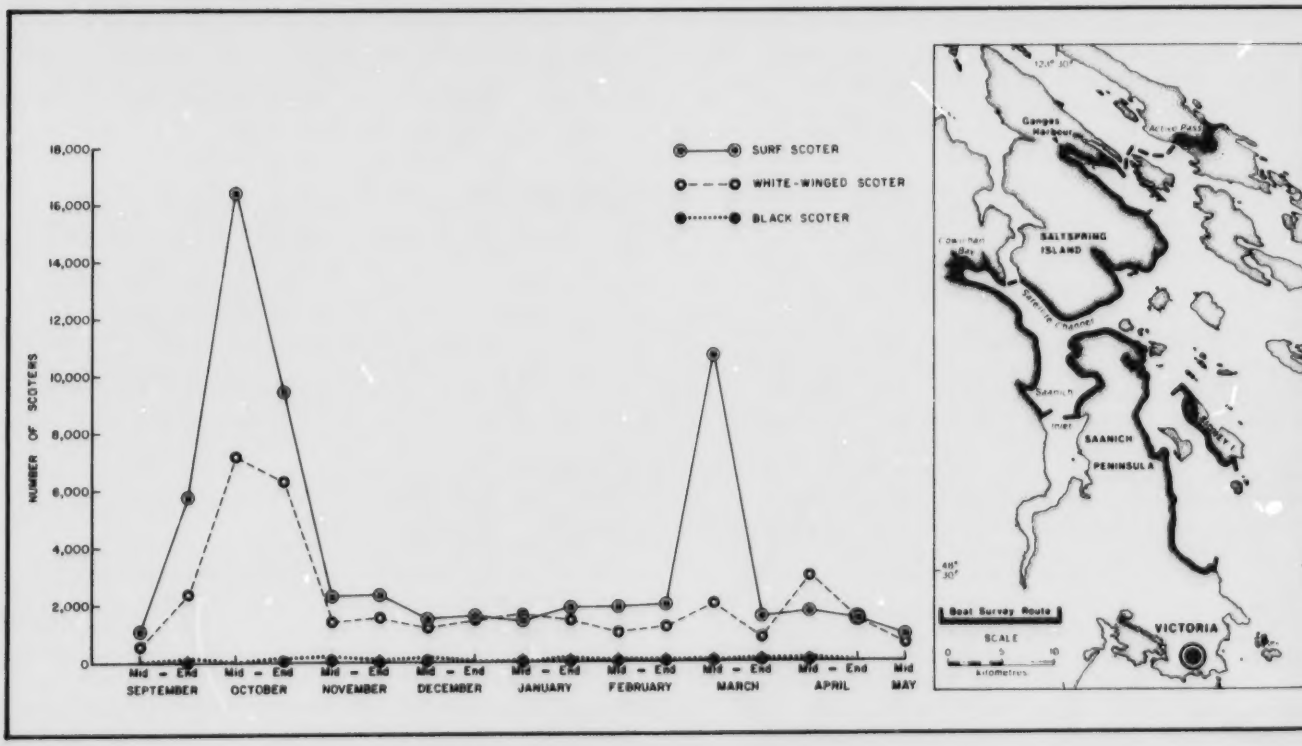
5.2.3. *Prey size* — White-winged Scoters select different-sized bivalves than Surf and Black scoters. Because size of scoter prey varies between regions (Vermeer 1981), valid comparisons for prey size can be only made for the same locations. At Saltspring Island the average length and standard error of 11 blue mussels from White-winged Scoters was 3.4 ± 0.4 cm whereas 218 blue mussels from Surf Scoters averaged 1.6 ± 0.04 cm long. At Denman Island the average length of 60 Manila clams from White-winged Scoters was 3.0 ± 0.2 cm whereas 38 Manila clams from Surf Scoters averaged 1.9 ± 0.2 cm in length. The mussels and clams eaten by White-winged Scoters averaged significantly larger than those taken by Surf Scoters ($P<0.05$). On the Fraser Delta, 85 blue mussels from Surf Scoters averaged 2.0 ± 0.08 cm long, compared to 19 blue mussels from Black Scoters which averaged 1.9 ± 0.2 cm in length. The Surf Scoter therefore feeds on similarly-sized mussels as the Black Scoter. It is not surprising that the White-winged Scoter takes larger bivalves than Surf and Black scoters as the former is much larger than the other two species, which resemble each other more closely in body weights. The mean weights, standard errors and numbers of scoters sampled were as follows: White-winged Scoter, 1722 ± 51 g (21 males) and 1437 ± 46 g (19 females); Surf Scoters, 1153 ± 12 g (64 males) and 1025 ± 15 g (26 females); Black Scoters, 1268 ± 10 g (25 males) and 1135 ± 49 g (7 females).

The similar size of their food items and overlap in prey species suggests interspecific competition between Black Scoters and Surf Scoters in which the latter are more successful in British Columbia. Black Scoters are numerous in the Aleutians and northern Europe where Surf Scoters are scarce or absent. In northern Europe, blue mussels are also a principal food of Black Scoters (Madsen 1954, Nilsson 1972). More information is needed to clarify the ecological relationship between Black and Surf scoters.

Table 3
Percentage occurrence of food items in scoter species at three British Columbia locations (sample number of scoters in parentheses)

	Denman Island			Fraser Delta			Saltspring Island	
Food species	**White-winged (*N* = 125)**	**Surf (*N* = 72)**	**Black (*N* = 15)**	**White-winged (*N* = 30)**	**Surf (*N* = 58)**	**Black (*N* = 13)**	**White-winged (*N* = 28)**	**Surf (*N* = 22)**
Bivalves	91	93	93	90	83	100	96	95
Mytilus edulis	29	53	93	10	38	38	11	68
Tapes philippinarum	60	58	13	10	3	—	—	—
Protothaca staminea	54	36	20	17	10	—	—	5
Clinocardium nuttalli	6	8	—	30	2	8	43	—
Mya arenaria	—	—	—	7	10	23	—	—
Saxidomus giganteus	4	—	—	—	—	—	43	—
Acila castrensis	—	—	—	—	—	—	21	—
Gastropods	34	17	13	63	17	15	39	9
Batillaria attramentaria	4	4	—	37	7	8	—	—
Littorina scutulata	18	1	7	—	—	—	7	—
Nassarius mendicus	8	3	—	3	—	—	11	—
Mitrella guasapata	2	1	—	—	—	—	18	—
Barnacles								
Balanus glandula	40	18	60	13	2	15	7	9
Polychaetes	—	1	—	3	12	46	—	—

Figure 5
Comparison of scoter numbers as observed by boat in Canadian Gulf Islands and adjacent Vancouver Island, September 1977 – May 1978



6. Acknowledgements

The authors thank the Institute of Ocean Sciences, Patricia Bay, for making boats available for bird surveys. B. Eccles and M. Morris of Queen Charlotte City collected and dissected scoters from Cumshewa Inlet. D.B. Quayle and F.R. Bernard of the Pacific Biological Station at Nanaimo, assisted with the identification of White-winged Scoter food as well as with information on the distribution and abundance of bivalves and gastropods in the study areas. P.F. Springer and D. Derksen reviewed the manuscript and made pertinent comments. The study was sponsored by the Canadian Wildlife Service and the Pacific Biological Station, Nanaimo.

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Feeding ecology of Black Brant on the north slope of Alaska

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1. Abstract

The feeding ecology of Black Brant (*Branta bernicla nigricans*) in their summer habitat was studied on the North Slope of Alaska from May to September 1978. The birds began arriving on the North Slope in late May. Breeding adults set up nesting territories on islands in coastal lakes and rivers. During nesting, males spent 22% and females 9% of the time feeding, primarily on *Carex aquatilis, Dupontia fischeri*, and mosses (sp. unknown). Non-breeders spent the early summer in arctic salt marshes where they fed on *Carex subspathacea* and *Puccinellia phryganodes*. In mid August, migrating brant frequented salt marshes where they spent 77% of the average 16-h daylight period in foraging at an average rate of 83 pecks/min. By the use of three different methods, food intake was estimated at an average of 305 g dry weight/day. Grazing pressure on arctic salt marshes was calculated at 374 brant-days/ha.

2. Résumé

De mai à septembre 1978, nous avons étudié l'écologie alimentaire de la Bernache noire (*Branta bernicla nigricans*) dans son habitat estival sur le versant nord de l'Alaska. Les oiseaux ont commencé à arriver en cet endroit à la fin de mai. Les adultes reproducteurs ont établi leurs territoires de nidification sur les îles parsemant les lacs et les rivières côtiers. Durant la nidification, les mâles passaient 22 % et les femelles 9 % de leur temps à se nourrir surtout de *Carex aquatilis*, de *Dupontia fischeri* et de mousses (espèces inconnues). Les oiseaux non reproducteurs ont séjourné au début de l'été dans les marais salants arctiques où ils se nourrissaient de *Carex subspathacea* et de *Puccinellia phryganodes*. À la mi-août, les bernaches en migration fréquentaient les marais salants où elles consacraient 77 % de la période diurne moyenne de 16 h à fouiller à un rythme moyen de 83 coups de becs par minute. À l'aide de trois méthodes différentes, nous avons estimé la consommation alimentaire à une moyenne de 305 g de poids sec par jour. La pression de broutage sur les marais salants arctiques a été calculée à 374 bernaches-jours par hectare.

3. Introduction

Oil exploration and development along the North Slope of Alaska pose a potential threat to coastal habitats and the animal populations they support. Thousands of Black Brant annually migrate to lakes and rivers there to nest, raise their young, and undergo an annual moult of body feathers (Owen 1980). Equally large numbers of non-breeding brant also moult along the North Slope (Derksen *et al.* 1979). Coastal salt marshes in the area serve as foraging sites for non-breeding brant during spring migration and for breeding birds, young, and non-breeders in the fall. In the event of an oil spill, brant using the marshes could be severely disrupted during critical foraging periods in their yearly cycle.

Geese, as grazers, must process large amounts of vegetation daily; however, they lack the complex digestive tract of ruminants, and little more than cell solutes may be absorbed by the intestines (Mattocks 1971). Geese, therefore, may exhibit adaptive behaviour which allows for the selection of plants of high nutritional quality.

Black Brant experience further constraints. As specialized feeders they select only a few plant species that are highly localized along the Pacific coast of North America. In addition, they are considered to be relatively inflexible in their feeding habits (Gabrielson and Lincoln 1959).

Several investigators (Harwood 1975, Owen 1972*a*, Owen *et al.* 1977, Lieff *et al.* 1970) have studied food selection by geese. To my knowledge, however, food intake has never been estimated for wild geese during the summer or while migrating. In order to obtain information on the threat that oil development on the North Slope might pose to the coastal habitats of Black Brant, a study of the birds was conducted from late May to September 1978. The objectives were to determine consumption and foraging routines, food selection, and grazing pressure in arctic salt marshes.

4. Study sites

Studies were conducted at two principal sites (Fig. 1). The first was at Anachlik Island, one of a few tundra-bearing islands in the aggrading Colville River delta (150° 24′ N, 70° 26′ W), which reaches Harrison Bay in the Beaufort Sea. The study site was a wetland habitat of about 300 m^2 on the northwest shore of the island where a series of drowned polygonal ridges becomes part of a complex lake. Within the lake, humps of exposed ridges form a system of small islands. One or two pairs of brant nested on each of these islands, making a total of 26 pairs at the site. *Carex aquatilis, Dupontia fischeri*, and moss (sp. unknown) were the dominant plants in the region.

The second site was a salt marsh along the mouth of the Putuligayuk River (148° 30′ N, 70° 19′ W). *Puccinellia phryganodes* and *Carex subspathacea* were the dominant plants in the marsh which lined the eastern and western shores

and covered a small island in the mouth of the river. Total area of vegetated salt marsh was about 1 km^2 (Fig. 1). Flocks of up to 250 migrating brant fed here for periods of from several hours to 2 days in the late summer.

In addition, counts of brant droppings were made at four other salt marshes on two occasions. Two of these marshes were in the Colville River delta, another was along the mouth of the Kalubik River, and the fourth was due west of West Dock, Prudhoe Bay, Alaska (Fig. 1). Dropping counts were also made at the Putuligayuk River salt marsh.

5. Methods and materials

5.1. Consumption and foraging routines

The first of three methods used in determining food intake consisted of five feeding trials with two 38-day-old brant carried out every 2–4 days from 16 to 26 August. At the time of capture the goslings weighed 60.8 g and 62.3 g, respectively. They were reared on local vegetation until they reached adult weights of 1335 g and 1420 g, respectively, on 20 August. The brant were held in 1-m by 2-m by 1-m wire pens where they remained for 24 h. Known quantities of saltmarsh vegetation were given the captive birds, along with water and a weighed pan of gravel. At the end of the 24-h period the vegetation and grit remaining in the pen and the feces were collected and weighed. The weight of food left in the pens was subracted from the weight of food supplied to the birds to give a measure of consumption during the experiment. Brant weight was recorded before and after each trial.

The second method involved observing the percent of time spent in foraging, the feeding rate (in pecks per min), and the amount of vegetation taken per bite by migrating and captive brant.

At the nesting colony on Anachlik Island, Black Brant were observed with a 20–60X zoom spotting scope at a distance of about 50 m. The population was scanned every 15 min, and the activity of each bird was recorded as outlined by Henry (1980) and Altman (1974). Observations were made from the time the brant arrived on the nesting ground on 1 June until they left the nesting area on 12 July.

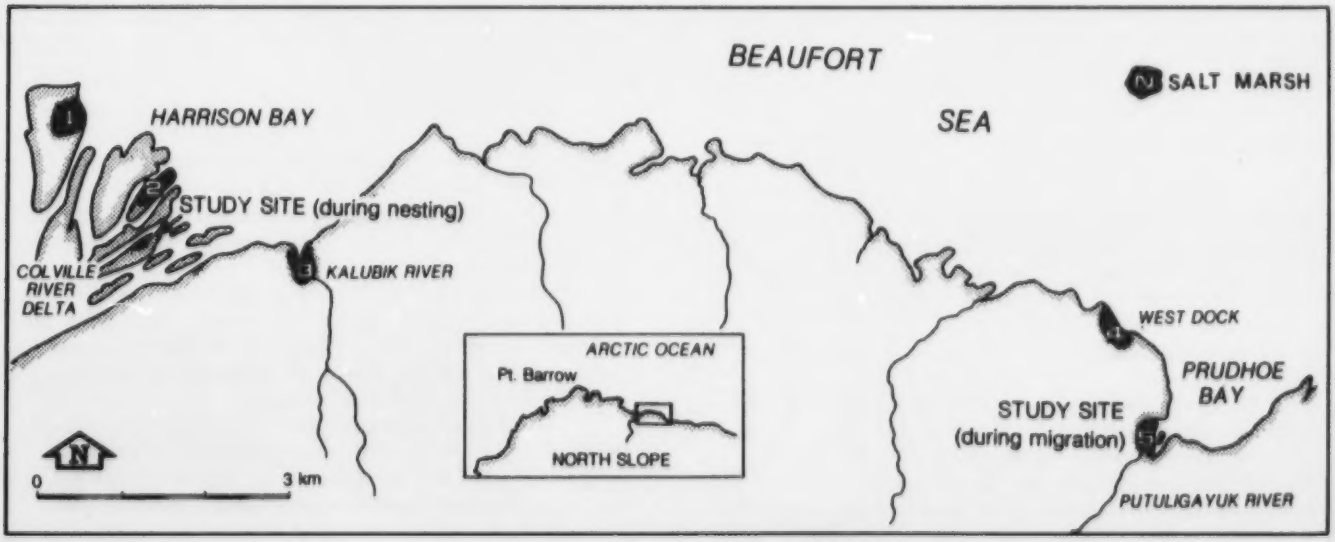
From 17 August until 7 September similar observations were carried out on flocks of geese at the Putuligayuk salt marsh. Because the distance from the flocks (200 m) and the number of individuals were large, feeding was the only behaviour that was generally noted. The population was scanned every 5 min with the telescope. Birds whose heads were lowered were counted as feeding; and those that were swimming, flying, or had their heads up were listed under the general category of other behaviour. The time taken for 50 pecks was measured in between scans for feeding behaviour.

Observations were also made on the feeding behaviour of the imprinted brant in the Putuligayuk marsh between 18 August and 1 September on days other than when the feeding trials were conducted. Bite size was estimated by watching one of the imprinted birds feed and by counting the number of bites taken. After feeding, the number of graminoid blades clipped by the bird was counted, and the lengths of unclipped as well as clipped blades were measured with a centimetre ruler. This gave a value for number and length of blades taken in each bite. Dry weight per unit length of graminoids was also measured. Graminoid vegetation refers to both grasses and sedges.

Multiplying the percent of foraging time by feeding rate and this value by the size of bite gave an estimate of consumption for wild birds and a second value for the imprinted brant.

The third method for estimating consumption is outlined by Ebbinge *et al.* (1975). Physiological studies indicate that cellulose digestion is quantitatively insignificant in geese (Mattocks 1971). Therefore, the relative content of cellulose in the food and in the droppings can be used as an indicator of digestibility. By knowing the daily fecal output,

Figure 1
North Slope of Alaska showing study sites during nesting and migration. Numbers in salt marshes designate areas used in the grazing pressure study



and the proportion of crude fibre in the food and that rejected in the feces, the rate of use of the food on a dry-weight basis can be calculated.

Fecal output was measured by weighing the droppings produced by the imprinted brant in the 24-h consumption trials. In the field,the feces produced in an hour by the imprinted birds were collected and weighed. Goose droppings from areas where wild geese had fed for a known amount of time were counted, collected, and weighed to give a third estimate of fecal output. Rate of food use was calculated by the formula of Ebbinge *et al.* (1975):

$$\% \text{ use (dry weight)} = 1 - \frac{M_r}{M_d} 100\%$$

where M_r = grams of marker substance (crude fibre) per 100 g food (dry weight), and M_d = grams of marker substance per 100 g of droppings (dry weight). Food intake was then calculated by using the following formula:

$$\text{Food intake} = \frac{DW}{1 - \frac{\% \text{ use}}{100\%}}$$

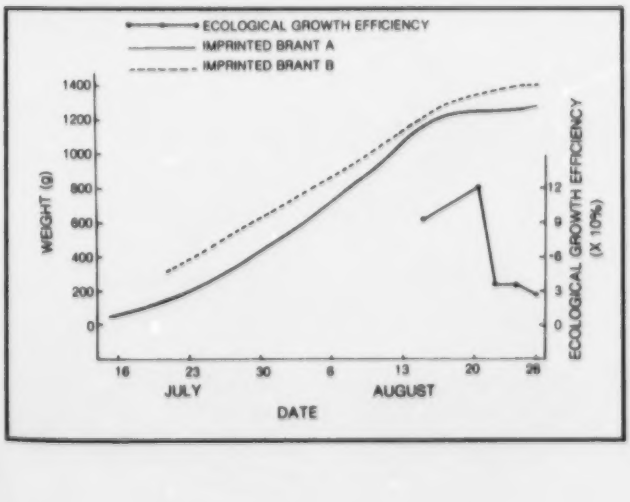
where DW = grams dry weight of droppings produced per day.

The three methods used for measuring consumption were applied only to fall-migrating brant and the imprinted geese feeding on saltmarsh vegetation. All values for food intake in the tables and throughout the text are given in grams dry weight of vegetation per day.

5.2. Food selection

Plants collected during the field season were identified according to Hulten (1968). During the feeding trials, *Carex subspathacea* and *Puccinellia phryganodes*, the main foods of migrating brant in this study, were provided to each of the captive goslings in separate food boxes and the relative proportion of each species eaten was determined. In addition, *C. subspathacea* and *P. phryganodes* were collected from areas where brant rarely grazed throughout the season.

Figure 2
Growth (in grams gained per day) of imprinted Black Brant, and ecological growth efficiency during the feeding trials



Samples were weighed, dried at 60°C for 24 h, and reweighed. Calculations for percent water content were made on these data. The dry samples were brought back from the Arctic for protein, fat, ash, and crude fibre determinations.

5.3. Grazing pressure

Five salt marshes (Fig. 1) were visited on 18 July before brant began migrating and on 7 September after the major migration was over. Counts of brant droppings were made with a 0.25-m^2 quadrat dropped randomly throughout the salt marsh. Total area of each salt marsh was obtained by means of a 50-m tape and maps. Knowing the average number of droppings per 0.25 m^2, the size of the marshes, and daily fecal output by brant, I calculated brant-days per marsh and grazing pressure in brant-days/ha. (Brant-days are the total number of brant visiting a marsh times the days they spent there.)

5.4. Laboratory methods

Samples were ashed according to the methods of the Association of Official Analytical Chemists (Horuity 1975).

Crude fibre was measured by means of the acid-detergent method (Van Soest 1962). Birds with gizzards consume quantities of sand and gravel regularly. Wild geese are no exception. Because no commonly used crude-fibre method extracts other ashable components and grit and because brant droppings contained large and varying percentages of grit, I ashed the crude-fibre extract to obtain an ash-free determination as well as to measure the unashed crude-fibre extract.

Fecal and vegetation samples were analysed for nitrogen by means of the micro-Kjeldahl method (Joslyn 1970). Protein was calculated by multiplying nitrogen by 6.25.

Calorimetric measurements of *Carex aquatilis*, *Carex subspathacea*, and *Puccinellia phryganodes* were obtained by means of a Parr bomb calorimeter (Schoemaker *et al.* 1974). Kilocalories were determined for the green blades of *Zostera marina* collected on 20 June 1979 in Puget Sound, Washington. Caloric values of *Zostera* do not vary significantly throughout the year or in different localities, and thus these values are comparable to those obtained for arctic graminoids eaten in the summer by brant (McRoy 1970).

6. Results

6.1. Consumption and foraging routines

The results of the five feeding trials are shown in Table 1. The amount of food consumed by the birds increased by more than 1.5 times during the trials, although the geese had reached adult weight of 1.25 kg and 1.35 kg (Morehouse 1974, Boyd and Maltby 1980), respectively, by the second trial and further weight changes were minimal (Fig. 2). By the third feeding trial the weight gain per weight of food eaten (ecological growth efficiency) decreased. The goslings mastered flying by 20 August.

The values on wild birds in Tables 2 and 3, and in Figure 3 were derived from data collected prior to and during nesting, and during migration. They could not be used to estimate consumption quantitatively as I was unable to measure the size of a bite taken by nesting brant (method 2) or collect feces in the lake region where they nested

(method 3). The figures, however, are useful in that they allow a comparison of activity patterns and foraging routines during different times in the summer season when the birds were engaged in different activities (arrival on nesting grounds, nesting, and migrating).

Upon arrival at the nesting grounds, brant fed 28% (SD = 15.4, N = 67) of the 24 h of daylight (Table 2). More time was devoted to resting, alert behaviour, and aggressive intraspecific interactions than at other times in the summer. They fed less between 00:00 and 06:00 (16% of the time, SD = 11.8, N = 5). Feeding increased throughout the morning and reached a peak in late afternoon between 14:00 and 17:00 (Fig. 3).

During nesting the percentage of time spent feeding dropped to 22% for males and the occasional female off the nest (see note in Table 2). All other activities except nesting also decreased. During the migration period the imprinted brant spent 64% (SD = 14.9, N = 52) of the time feeding, whereas wild birds fed significantly more of the time (77%, SD = 22.4, N = 148, F-test, $P<0.05$) (Table 3).

During nesting, females fed 9.4% of the time (Table 3). Other observations I made indicate they left the nest an average of eight times a day and fed for an average of 18 min each day. Seventy-four percent of their feeding took place between 08:00 and 11:00 and 14:00 and 17:00. They took an average of 100 pecks per min. Males plus females off their nest during the nesting season fed 22% of the time at a rate significantly slower than that of nesting females, 75 pecks per min (F-test, $P<0.05$). They fed sporadically throughout the day, with a slight increase of feeding activity between 10:00 and 12:00 (Fig. 3).

Brant observed during the migration period spent 77% of the average 16 h of daylight in foraging during late August and early September. Adults fed at an average rate of 83 pecks/min whereas juveniles pecked significantly faster, taking 103 pecks/min (Table 3). I was unable to definitely distinguish between adults and juveniles while scanning the flock for percent foraging time. When counting pecks/min in between scans, I located isolated family groups in which the age differences were readily visible and based my data for juveniles on these observations. The wild birds fed most heavily in the morning and significantly less as the day passed (F-test, $P<0.05$) (Fig. 3). In late August the imprinted brant fed an average of 64% of the time, taking 91 pecks/min. The amount of time they spent feeding did not decrease significantly throughout the day (F-test, $P>0.05$).

Based on pecks/h, males (see note on Table 3) fed almost twice as much as females during nesting. During the migration period, brant fed about 3.5 times as much as birds off the nest during the nesting period, with the imprinted geese averaging slightly less than the wild birds (Table 3).

The length of a graminoid blade that brant ate depended upon the height of the plant. *Carex aquatilis* by the

Table 1
Amount of vegetation (g dry weight/day) consumed by two imprinted Black Brant in feeding trials in August 1978

Date	Brant A	Brant B
16 August	266	281
20 August	235	235
22 August	275	337
24 August	355	492
26 August	473	465
$\bar{x}$ food intake	341.4	
SD	101.0	
N	10	

Table 2
Time budget (percent time spent in different behaviours) of wild Black Brant before and during nesting*, and of imprinted Black Brant in the late summer

	Pre-nesting	Nesting	Imprinted brant
Dates	1 – 12 June	13 June – 12 July	18 Aug. – 1 Sept.
Hours observed	20	24	26
Foraging	28	22	64
Alert	19	12	—
Nesting	0	40	0
Resting	28	14	11
Preening	7	4	11
Interaction	10	2	—
Swimming	4	2	—
Flight	3	1	—
Other	1	3	14
Totals, %	100	100	100

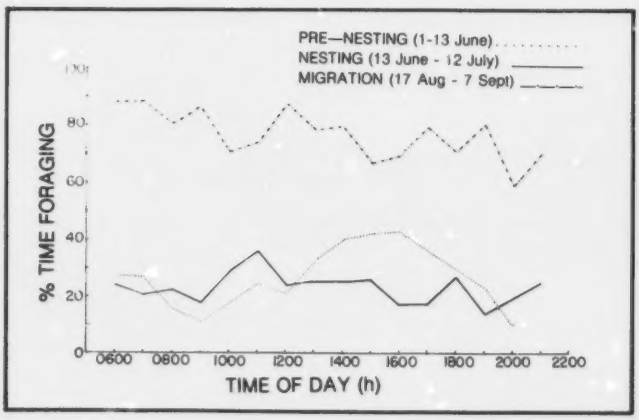
*Counts before nesting based on both males and females. Counts during nesting based on all birds except six nesting females, but could have included some females off their nests.

Table 3
Feeding rate of Black Brant at several times during the summer season

	Nesting, 13 June – 12 July		Migrating, 17 Aug. – 7 Sept.		Imprinted brant, 18 Aug. – 1 Sept.	
	Females*	Males†	Adults and juveniles	Juv.	A	B
% time foraging	9.4	21.7	77.3	‡	66.8	60.8
Pecks/min	100§	75§	83§	103§	85	97
SD	18.0	17.2	7.0	13.5	10.5	12.7
N	109	79	489	29	93	88
Pecks/h¶ (effective)	564	977	3850	—	3407	3540

*Based on six nesting females.
†Based on all birds except the six nesting females. Counts could have included some females off their nests.
‡Data incomplete as juveniles within flock were not always distinguishable from adults.
§$P<0.05$, F-test.
¶Pecks/h = pecks/min × 60 min × percent time foraging.

Figure 3
Daily foraging pattern exhibited by Black Brant at three different times in the summer season



end of nesting season had attained a height of about 60 mm. The geese broke off an average of 35 mm (SD = 10.3, N = 148) of the blade in a bite.

Saltmarsh vegetation is much shorter than that found in the tundra. The brant took bites of blades of *Carex subspathacea* and *Puccinellia phryganodes* that were an average of 19 mm (SD = 6.6, N = 93) and 13 mm (SD = 5.3, N = 95) in length, respectively. In many places in salt marshes, vegetation was clipped to within 15 mm of the ground. On the average, the geese ate 2.9 (SD = 0.85, N = 21) blades in each bite of *C. subspathacea* and 2.5 (SD = 0.92, N = 21) blades of *P. phryganodes*. The dry weight of saltmarsh graminoids, averaged over the season, that was taken in one bite was 3.1 mg (SD = 0.6 mg, N = 6). Multiplying the weight of vegetation taken in one bite by the feeding rate and percent time spent foraging, I estimated consumption by the migrating birds at 283 g/day and by the imprinted brant at 250 g/day (Table 4). These values were calculated on an assumed 24-h feeding period. It is generally believed that most geese do not feed at night unless there is a full moon (Ranwell and Downing 1959, Owen 1972*a*, Ebbinge *et al.* 1975, Henry 1980). Burton and Hudson (1978), however, have reported that the feeding activity of Lesser Snow Geese is dependent on tidal fluctuations, and night-time feeding is common in winter during low tides, regardless of light intensity. I based my calculations on the fact that the imprinted brant fed at night at the same rate as during the day. Geese, when they do feed in the dark (Owen 1976), probably forage at a slower rate than during the day because of a necessary increased alertness for predators. I had no way, however, of estimating a night-time feeding rate. Therefore, my values should be considered as maximum estimates of food intake.

The crude fibre method as outlined by Ebbinge *et al.* (1975) gave a consumption of 375 g/day for birds on the North Slope (Table 4). The crude fibre extract from both the fecal and graminoid samples, however, contained large and varying amounts of grit and other refractory components. Although the data obtained from the crude fibre analysis appeared reasonable when compared with the other estimates of consumption, they had to be discounted because of the presence of grit. To correct for this error, I ashed the crude fibre extract and calculated a new estimate of consumption of 352 g/day and 299 g/day for the imprinted brant and wild brant, respectively.

Table 4
Amounts of vegetation consumed by imprinted and wild Black Brant as estimated by three different methods (standard deviation and number of samples in parentheses)

	$\bar{x}$ consumption of vegetation, g dry-wt/day	
	Imprinted brant	**Wild brant**
Method 1 (feeding trials)	341 (101, 10)	—
Method 2 (field observations)	250	283
Method 3 (ash-free crude fibre)	352 (36, 4)	299 (60, 4)
(crude fibre)	374 (17, 4)	376 (82, 6)
$\bar{x}$	305.5*	
SD	42.98	
N	5	

*Method 3 (crude fibre) not averaged in with other values because of presence of grit in samples.

The caloric value for several arctic graminoids are given in Table 5. They are somewhat higher than the value of 3.3 kcal/g that I determined for *Zostera marina*, the principal winter food of Black Brant (Cottam *et al.* 1944, Henry 1980).

C. subspathacea and *P. phryganodes* were of a comparable nutritional quality. *C. aquatilis* had a consistently higher protein content than either of the saltmarsh graminoids. Both *C. subspathacea* and *P. phryganodes*, however, had a significantly higher moisture content than *C. aquatilis* (F-test, $P<0.05$) (Table 5).

Analyses of *C. subspathacea* collected at different times during the summer indicated that nitrogen content increased from mid June to mid August and declined thereafter (Table 6). Samples of *P. phryganodes* showed a gradual, although not consistent, decline in nitrogen content. The mean values for nitrogen content in *C. subspathacea* was 1.73 (SD = 0.26, N = 5) and in *P. phryganodes*, 1.86 (SD = 0.28, N = 4). Water content in *C. subspathacea* increased from August to September, whereas in *P. phryganodes*, water content increased until 22 August and thereafter remained the same (Table 6). Fat content in *C. subspathacea* generally decreased throughout the season.

Table 5
Proximate analysis of three plants and of Black Brant droppings. (All values are based on dry weights and are averages for the summer. Standard deviation and number of observations are given in parentheses. Superscripts denote significant differences where letters are paired [t-test, $P<0.05$])

	Carex aquatilis	*Carex subspathacea*	*Puccinellia phryganodes*	Brant droppings
% water content	49[a,b] (15.9, 13)	73[a] (7.8, 4)	72[b] (4.8, 4)	82 (6.4, 9)
% ash	9.0[c,d] (6 7, 8)	10.5[c] (4.0, 5)	11.3[d] (2.0, 4)	15.5 (6.4, 26)
% fat	—	5.28 (1.0, 5)	—	3.78 (1.2, 3)
% nitrogen	3.2[e] (1.1, 5)	1.7[e] (0.26, 5)	1.9 (0.28, 4)	1.6 (0.39, 13)
% protein (nitrogen × 6.25)	20.2	10.6	11.9	9.7
kcal/g	4.3	3.7	3.6	—
% crude fibre	24.5[f] (1.0, 4)	16.5[f] (0.71, 4)	19.4 (4.2, 4)	25.5 (3.7, 21)
% ash-free crude fibre	18.3[g] (4.9, 6)	3.8[g] (1.0, 4)	10.1 (7.2, 4)	16.2 (5.4, 16)

Table 6
Variation in nutritional characteristics of *Carex subspathacea* through the summer and of *Puccinellia phryganodes** in late summer 1978. (All values are given as percentages based on dry-weight measurements. Standard deviation and number of observations are given in parentheses. Superscripts denote significant differences where letters are paired [t-test, $P < 0.05$])

	Water content		Nitrogen		Fat	
Dates	***C. sub.***	***P. phr.***	***C. sub.***	***P. phr.***	***C. sub.***	***P. phr.†***
15 June	†	†	1.65[a] (0.21, 2)	—	6.27[g] (0.08, 2)	—
14 Aug.	65	65	2.17[a,b,c] (0.08, 2)	2.15[e] (0.05, 2)	4.75 (2.53, 4)	
22 Aug.	76	76	1.50 (0.71, 2)	1.67 (0.21, 2)	5.0 (1.72, 4)	—
26 Aug.	69	74	1.69[b,d] (0.02, 2)	2.06[d,f] (0.13, 2)	5.75 (1.77, 2)	—
4 Sept.	83	73	1.62[c] (0.08, 2)	1.58[e,f] (0.13, 2)	4.13[g] (0.39, 2)	—

**Puccinellia phryganodes* was not collected on 15 June, when it was covered with water from the Putaligayuk River during spring thaw.
†Analysis not performed.

Table 7
Brant-days and grazing pressure in several arctic salt marshes

Salt marsh no.	Droppings/m² 18 July – 5 Sept.		Brant-days/marsh	Brant-days/ha
1	2.56	13.6	109,975	425
2	0	9.2	3,539	354
3	2.72	*	—	—
4	0	12.4	768	379
5	4.4	14.4	19,231	385
$\bar{x}$ brant-days/ha				385.75
SD				29.40
N				4

*Droppings washed away when river flooded.

6.2. Food selection

When brant first arrived at the nesting area, the ground was still partially covered by snow, and little green vegetation was available. During this time I observed them feeding on mosses (sp. unknown), fresh water algae (sp. unknown), *Equisetum variegatum*, and old seed heads of *C. aquatilis*.

During nesting I observed the brant feeding predominantly on *C. aquatilis* and *Dupontia fischeri*. The vegetation around the nesting area was clipped level with the ground. On the islands where the nests were located, graminoids were sparse and here a lush ground cover of moss grew. On warm days when many adult insects were emerging, I observed brant apparently feeding on chironomids (*Chironomus* spp.) which were in windrows along the lake's edge. The birds skimmed the water's surface with their opened bills, seemingly collecting hundreds of the insects.

The imprinted brant frequently accompanied me out in the field where they were free to select any vegetation available. In the salt marsh along the Putuligayuk River they invariably ate *C. subspathacea* and *P. phryganodes* in the salt marshes. To see if they preferred one of these graminoids over the other, I measured the amount of each that the imprinted brant ate in the feeding trials. The two birds ate an average of 707 g (SD = 600, $N = 5$) and 550 g (SD = 172, $N = 5$) of *P. phryganodes*, and 530 g (SD = 135, $N = 5$) and 658 g (SD = 104, $N = 5$) of *C. subspathacea*. A t-test on the results showed that the brant did not significantly choose either *C. subspathacea* or *P. phryganodes* over the other ($P > 0.05$).

6.3. Grazing pressure

Between 13 and 18 June, 10–20 non-breeding brant fed along the Putuligayuk River (Fig. 1, salt marsh #5). From 19 to 24 June, 60 non-breeding brant were seen feeding in a salt marsh in the Colville River delta (Fig. 1, salt marsh #2). These geese were probably second- or third-year birds that had migrated to the North Slope to moult. By the beginning of July, non-breeders had left the salt marshes, presumably for inland lakes where they moult. Thirty-two thousand non-breeders spent from July to early August in the Lake Teshepuk region, 120 km west of Prudhoe Bay, on the western shores of Harrison Bay. By early August, moult was completed and the brant moved to coastal habitats (Derksen *et al.* 1979).

The brant nesting on Anachlik Island left the area as soon as the young were hatched. They were seen occasionally in the Colville River delta for about 1 month (Jim Helmerick, pers. commun.). Paired brant and family groups were seen infrequently in salt marshes near Prudhoe Bay from mid July to mid August. At this time of year they were moulting and, therefore, flightless, and swam out of sight before I could observe them feeding. On 27 July I flew an aerial survey from Flaxman Island to the Kuparuk River and counted 200 brant in small groups at the mouths of rivers.

The first flock of adults and young of the year was seen on 17 August when 1300 birds flew west past Oliktok, 35 km northwest of Prudhoe Bay (Katie Hirsch, pers. commun.). On 18 August a small flock of 25 brant landed in the Putuligayuk salt marsh and fed for several hours. From then until 7 September, when I left the North Slope, flocks of up to 250 brant stopped and fed along the Putuligayuk River for as long as 2 days. The peak migration in 1978 passed Simpson Lagoon, 30 km west of Prudhoe Bay, on 17 – 31 August, and in 1977, on 22 August – 6 September. The total number of brant migrating west past Simpson Lagoon was estimated to be 4638 in 1977 and 11 000 in 1978 (Johnson 1979).

Over a 19-day period, I observed 861 brant feeding in the Putuligayuk salt marsh. This resulted in a grazing pressure of 327 brant-days/ha. The imprinted and migrating birds produced an average of 237 droppings/day (SD = 54.7, $N = 16$). From the area of the salt marshes, the average number of droppings/m², and the number of droppings produced in a day, I calculated an average grazing pressure of 386 brant-days/ha (Table 7), SD = 29, $N = 4$). Based on this value and the 19-day observations, the average brant-days/ha was 374 (SD = 36.6, $N = 5$). By converting hectares to square metres and dividing by the average number of brant-days, one brant would feed from 26.7 m² in a day. A brant consuming about 305 g/day (Table 4) would take 11.4 g dry weight of vegetation per square metre.

7. Discussion

7.1. Feeding ecology

Barry (1956) noted brant feeding on *Equisetum* sp. and unidentified grass shoots before nesting in the Canadian Arctic. He reported that during nesting they fed on *Puccinellia phryganodes* around the nests. After the young had hatched, the adults led them to coastal mudflats where the flock fed on small crustaceans and small invertebrates. I observed brant prior to nesting, feeding on mosses (sp. unknown), freshwater algae (sp. unknown), *Equisetum variegatum*, and old seed heads of *Carex aquatilis*. During nesting, however, they fed primarily on shoots of *C. aquatilis* and *Dupontia fischeri*. Chironomids were taken on days of peak emergence. Derksen *et al.* (in press) reported that, based on examination of the droppings, non-breeding brant in the Lake Teshekpuk area fed primarily on mosses and to a lesser extent on *Deschampsia caespitosa* and *C. aquatilis*. Mosses grew lushly around brant nests on Anachlik Island, and it was quite likely that they fed on them, although I was not close enough to the nests to make direct observations.

In late summer, brant fed on *Carex subspathacea* and *Puccinellia phryganodes* in salt marshes along the arctic coastline (this study, David Mason, pers. commun.). The movement of brant to marshes from a tundra habitat can be theoretically associated with the need to maximize the quantity or the nutritional quality of the forage they are consuming (Krebs and Cowrie 1978).

Results of the nutritional analyses show the saltmarsh species, *C. subspathacea* and *P. phryganodes*, to have a significantly higher moisture content than the tundra species, *C. aquatilis*, and *C. subspathacea* to have a significantly lower fibre content than *C. aquatilis*. This suggests that saltmarsh plants are more easily ground up in the gizzard and, therefore, have a higher digestibility and greater nutrient availability. In addition, more food may be processed per unit time. Charman and Macy (1978) suggested the degree to which a plant could be ground up in the gizzard as a factor in food selection by brant wintering in England. Owen *et al.* (1977) reported that Barnacle Geese respond adversely to the brittleness of vegetation and thus selected, on a mechanical basis, the more tender plants with higher percentage of moisture.

Owen *et al.* (1977) also noted that the plants selected by geese had a higher nitrogen content than those not selected. Other investigators have also suggested that geese select foods to optimize nitrogen intake. Harwood (1975) reported that the blue race of Lesser Snow Geese fed most heavily in plots where vegetation had a significantly higher protein content than in other areas. Owen (1975) reported that Eurasian Greater White-fronted Geese selected fertilized vegetation with a 10% higher nitrogen content rather than vegetation in unfertilized plots. On the other hand, Lieff *et al.* (1970), in grazing trials with captive Lesser Snow Geese and Canada Geese, found no relationship between goose preference and the nutritional characteristics of the plants they chose. Owen (1972*b*, 1976) found a high rate of food intake by Eurasian Great White-fronted Geese to be more important than the nutritional qualities of the vegetation they selected. My results show that *C. aquatilis* had a significantly higher nitrogen content (3.2%) than *C. subspathacea* (1.7%, t-test, $P<0.05$). There was no significant difference between *C. aquatilis* and *P. phryganodes* (1.9%, t-test, $P>0.05$). Ulrich and Gersper (1978) reported nitrogen values in *C. aquatilis* of 2.9% in 1972 and 3.3% in 1973. Cargill (1981) found nitrogen content in ungrazed *P. phryganodes* to be 0.8 and 2.1% during August 1979 and 1980, respectively. For the same sampling periods she reported 1.3 and 3.0% nitrogen, respectively, in ungrazed *C. subspathacea*. These studies indicate that nitrogen content in arctic graminoids varies greatly from year to year and that the tundra species, *C. aquatilis*, generally has a higher nitrogen content than ungrazed saltmarsh vegetation. Cargill (1981), however, showed that grazing by Lesser Snow Geese increased the average total nitrogen content in saltmarsh vegetation. In samples collected in August she found grazed *P. phryganodes* to have a nitrogen content of 2.5% in 1979 and 2.8% in 1980, and grazed *C. subspathacea*, 3.0% in 1979 and 3.9% in 1980. I collected samples of vegetation from areas where grazing by brant was infrequent. The results, therefore, must be interpreted in this light, and no definitive statement can be made whether or not brant moved to salt marshes to maximize nitrogen intake. It is apparent, however, that saltmarsh graminoids had a higher moisture content and a lower fibre content than tundra vegetation, and brant may have been exploiting these characteristics in the plants they selected.

The results I obtained for food intake indicate that brant were maximizing the quantity of forage consumed during late summer. A mean value for consumption of 305 g/day (dry weight) was obtained from the three methods of estimating food intake. Based upon my caloric determination of food, this amounts to 1100 kcal/brant/day. This value for food intake varies from those of other investigators (expressed in grams dry weight/day). Sincock (1965) estimated food intake by wintering Atlantic Brant at 10% of body weight, or 150–180 g/day. Ogilvie (1978) gave an estimate of 135–158 g/day for Barnacle Geese wintering in England. Captive brant during the summer were estimated to use 306–367 kcal/bird/day (85–100 g/day) while feeding on commercial feed with a caloric value of 3.65 kcal/g (Morehouse 1974). The values given by Morehouse are not strictly comparable to values I obtained for unrestrained birds at normal field temperatures feeding on native vegetation, but they are of interest as the only values of food intake I have found for geese during the summer. Ebbinge *et al.* (1975), using the crude fibre method, estimated consumption by wintering Barnacle Geese at 135–160 g/day. In the same study, he compared grazed vegetation to ungrazed vegetation within an exclosure, and estimated a maximum food intake of 255–340 g/day. Since food intake varies with body weight of the bird, and since brant and Barnacle Geese both weigh approximately 1.3 kg, the values reported in the literature for these two species are likely to be similar. My results show that Black Brant during summer 1978 were consuming about twice as much food as brant and Barnacle Geese do in winter.

The values I obtained for droppings produced by a goose per day were similarly high compared to values reported elsewhere. Ebbinge *et al.* (1975) gave a value of 160 droppings, or 106 g dry weight, produced by wintering Barnacle Geese per day. Kear (1965) reported that geese excreted between 58 and 175 g dry weight of droppings per day, depending on the size of the goose. Owen (1972*a*) calculated that Eurasian Greater White-fronted Geese produced 150 droppings, or 110 g dry weight, in a day in which 9 h were spent actively feeding. Adult Lesser Snow Geese summering in the Arctic, produced 231 droppings in a day (Susan Cargill, pers. commun.). My imprinted brant and

those that were migrating produced 237 droppings (SD = 54.7, N = 16) with a mean dry weight of 1 g each. It is to be expected that if brant in the late summer are consuming more vegetation than in the winter, they would also be producing more droppings.

Behavioural traits of brant appear to be adapted to allow them to maximize food intake in the late summer when they are recouping the energy losses of summer and preparing for migration. The birds at the Putuligayuk salt marsh spent 77% of the average 16 daylight hours feeding. Although the number of daylight hours available to geese for foraging varies from season to season and place to place, several investigators have reported geese spending about three-fourths of the daylight period feeding. Kramer (1976), studying Black Brant wintering in Baja California, and Harwood (1977), working with Lesser Snow Geese in the Canadian Arctic, reported the birds feeding 77% of the daylight hours. In Humboldt Bay, California, brant fed 63.8% of the daylight period over the winter, and 80.4% during April prior to spring migration (Henry 1980). Owen (1972*a*), however, reported Eurasian Greater White-fronted Geese fed up to 90% of the daylight hours on their wintering grounds in England in a year when food was not plentiful. During moult, Black Brant on Alaska's North Slope fed 89–95% of the time (Derksen *et al.* 1982). Thus, in the long hours of arctic daylight, brant are able to maximize food intake by spending a high proportion of time in foraging.

Food intake may also be maximized by an increased rate of pecking. Females during nesting fed significantly faster than males. During the migration period, juveniles pecked at a significantly higher rate than adults. At both of these times, maximizing consumption within a given time period may be adaptive behaviour. Harwood (1975) found that Lesser Snow Geese spent more time feeding and pecked significantly faster in grazed areas than in ungrazed areas. Grazed vegetation had a higher protein content, and, thus, geese maximized both protein and food intake per time spent foraging, provided the take per peck in the two situations was comparable.

7.2. Grazing pressure and carrying capacity

Average grazing pressure by brant in four salt marshes along the central coast of the North Slope was 374 brant-days/ha. Based on this value and values for food intake, the birds consumed approximately 11.4 g dry weight of saltmarsh vegetation per square metre. Annual above-ground productivity of *C. subspathacea* in the Putuligayuk salt marsh has been measured at 33 g/m^2 in 1977 and 29 g/m^2 in 1978 (David Mason, pers. commun.). Geese were seen grazing in the area in which the measurements were taken, but grazing was light during the 2 years of the study. Brant would consume under these circumstances about one-third of the vegetation available in salt marshes, if it is assumed that grazing does not significantly increase productivity.

Several investigators have reported values for grazing pressure by wintering geese in lower latitudes. These values varied from 630 to 1500 goose-days/ha (Kuyken 1969, Owen 1972*b*, Ebbinge *et al.* 1975). Carrying capacity of grass pastures in the Netherlands was estimated by Ebbinge *et al.* (1975) at 2600 goose-days/ha and by Owen (1972*b*) in England at 1750 goose-days/ha, values two to three times higher than those of grazing pressure reported by the same investigators. In the Netherlands pastures Barnacle Geese would remove 40% of the standing crop of subarctic tundra vegetation. Kuyken (1969) noted a 34% decrease in standing crop from grazing by geese wintering in Belgium. During May on the Dutch island, Schiermonnikoog, brant removed 30% of *Plantago maritima* and *Puccinellia maritima* leaves. Clipping experiments showed a 30% removal of leaf material to result in the highest regrowth of new plant tissues (Prins *et al.* 1981). These values reported in the literature correspond well with those for brant in the Arctic and possibly represent the maximum vegetative removal without resulting in the overgrazing of an area. Cargill (1981), however, reported that Lesser Snow Geese removed 80% of the standing crop in low-latitude arctic salt marshes with no evidence of overgrazing. Nevertheless, grazing pressure at four salt marshes along the North Slope were amazingly consistent, indicating that brant were spacing their foraging in a manner that avoided overexploiting the vegetation.

8. Conclusions

Migration data from fall 1978 show 11 000 brant passing Simpson Lagoon (Johnson 1979). Thirty-two thousand brant migrated west from the Lake Teshekpuk area after moult in 1978, a number which has more than doubled since 1976 (Derksen *et al.* 1979). Thus, at least 42 000 birds are using salt marshes along the North Slope during fall migration.

Oil development is continually expanding along Alaska's northern shores. With development comes the constant threat of habitat destruction by oil spills, and of disturbance of foraging brant by human activity. Brant depend on arctic salt marshes during the season when their metabolic reserves are low and the energetic demands of migration high. This study shows that if the present number of birds are to continue to use the North Slope, oil development should proceed in a way such that salt marshes are protected from proximity to development and, in the case of an oil spill, every effort should be made to prevent oil from washing into salt marshes.

9. Acknowledgements

I am grateful to David Mason and A.C. Broad for valuable advice throughout the project. Thanks are also due to Jim and Tina Helmericks and the people associated with the Outer Continental Shelf Environmental Assessment Program in Fairbanks and Prudhoe Bay for logistic support. I appreciate the help of William Wilson, Crystal Driver, and Rai Peterson in the chemical analyses of my samples. I am grateful to Dirk Derksen for his interest in this project and for information on Black Brant and to Paul Springer for his editorial advice. Field work was done when I was employed by Western Washington University on National Oceanic and Atmospheric Administration Contract 03-5-622-81, and I am grateful to that program for financial support.

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Part II

Feeding ecology of pelagic marine birds

Phalarope feeding in relation to autumn upwelling off California

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1. Abstract

A joint ship-aircraft-satellite study conducted off central and northern California examined the relationship of phalarope feeding to convergences and other physical and biological processes of upwelling. Phalaropes were most numerous where strong surface thermal gradients bordered upwelling waters. Birds collected off Point Reyes and Point Montara had fed primarily on fish eggs and euphausiids, while off Davenport copepods were the predominant prey. Thaliaceans and siphonophores dominated the zooplankton collected in shallow, oblique tows within 40 km of the coast. Copepods and euphausiids replaced these gelatinous organisms farther offshore and were especially abundant at a convergence 30 km off Davenport. Fish eggs were rare in the tows, indicating phalaropes ate them outside of the area sampled. Although phalaropes tend to be attracted to surface manifestations of ocean convergences (e.g. slicks), not all convergent areas necessarily provide the right combination of hydrographic and biological conditions for sufficient prey concentrations. Specific temporal and spatial factors may ultimately determine the value of a given convergence as a source of prey.

2. Résumé

Une étude réalisée à la fois par bateau, avion et satellite au large du centre et du nord de la Californie nous a permis d'examiner le rapport entre l'alimentation des phalaropes et les convergences et autres phénomènes physiques et biologiques de la remontée des eaux profondes. Ces oiseaux étaient plus nombreux lorsque de forts gradients thermiques de surface bordaient les eaux résurgentes. Les oiseaux recueillis au large de Point Reyes et de Point Montara s'étaient nourris surtout d'oeufs de poissons et d'euphausiides, tandis qu'au large de Davenport, les copépodes étaient la proie prédominante. Les thaliacés et les siphonophores constituaient le gros du zooplancton recueilli dans les traits de filet obliques et peu profonds effectués à moins de 40 km de la côte. Les copépodes et les euphausiides remplaçaient ces organismes gélatineux plus au large et étaient particulièrement abondants à une convergence située à 30 km de Davenport. Nous trouvions rarement des oeufs de poissons dans les prélèvements, ce qui veut dire que les phalaropes les mangeaient à l'extérieur de la zone échantillonnée. Bien que ces oiseaux avaient tendance à être attirés vers les manifestations de surface des résurgences marines (par exemple, les nappes), toutes les zones convergentes n'offraient pas nécessairement la bonne combinaison de conditions hydrographiques et biologiques pour assurer une concentration suffisante de proies. Certains facteurs spatio-temporels peuvent finalement déterminer la valeur d'une convergence donnée comme source de proies.

3. Introduction

Several successful investigations during the past decade (reviewed in Ainley 1976, Ainley 1980, Brown 1980) have demonstrated that many aspects of seabird occurrence, colony productivity, and social structure relate directly to measurable offshore hydrographic and biologic processes. The advent of remote-sensing techniques, particularly from aircraft and satellites, to oceanographic studies (Arvesen *et al.* 1973, Bernstein *et al.* 1977, Stevenson *et al.* 1979) makes possible habitat-mapping over large ocean areas in very short time intervals, i.e. "synoptic coverage." Such techniques when coupled with standardized shipboard bird observations and hydrographic measurements, allow us to document and test hypotheses about the role of *mesoscale ocean features* (tens to a few hundreds of kilometres) in seabird ecology. This is probably the spatial scale of greatest importance to many pelagic and coastal marine birds.

This paper attempts to integrate phalarope feeding ecology and distribution with the biology and hydrography of autumn upwelling systems off California. Phalaropes are particularly suitable for such studies because they are easily seen from ship or air, they do not dive for food, are not quite as mobile as some pelagic birds, and they exploit a relatively limited neustonic food source (Ainley and Sanger 1979). Furthermore, unlike birds that return to shore each day and are affected by such factors as distance to colonies or large roosts, Red Phalaropes (*Phalaropus fulicarius*) spend most of the year away from the coast and can therefore be expected to respond directly to conditions offshore.

The affinity of phalaropes for upwelling regions is well known, and their concentration at surface convergences has been noted (Murphy 1936, Lamb 1964, Martin and Myres 1969, Ashmole 1971). Brown, in studies of the Senegal upwelling system (1979) and the Labrador Sea (1980), correlated the occurrence of Red Phalarope flocks with gradients in sea surface temperature (SST) and with the location of apparent offshore convergences. Brown (1980) also found that Red Phalaropes were most numerous at a topographically induced tidal divergence that upwelled zooplankton to the surface. He postulated that these birds actually *require* convergences or divergences to concentrate their minute, patchily distributed prey to exploitable levels. Brown suggested several physical mechanisms that might

concentrate planktonic prey for phalaropes, and utilized satellite imagery to map these physical features.

This paper reports the results of an experiment in which we could correlate phalarope occurrence with major habitat gradients while simultaneously examining phalarope feeding within an active upwelling system.

4. Study area and oceanographic setting

4.1. Study area

Our study area extended from the coast to 185 km offshore between Santa Barbara Channel and the California–Oregon border, comprising approximately 162 500 km^2 (Fig. 1). The continental shelf varies in width from about 10 to 75 km. Waters in in approximately 63% of the study area exceed 2000 m in depth, about 13% are shallower than 200 m, and the remainder includes continental slope waters of intermediate depth. Though the region's shelf-slope bathymetry is relatively uniform, significant anomalies in shelf topography (canyons, escarpments) exist off Point Sur, Monterey Bay, and Cape Mendocino.

4.2. Oceanographic setting

The general hydrographic characteristics of this region have been described by Reid *et al.* (1958), Bolin and Abbott (1963), and reviewed by Hickey (1979). The California Current is a wide (~1000 km), slow (to about 30 cm/s) current that flows equatorward, bringing cool low-arctic waters to the California coast. A poleward undercurrent (the California Undercurrent) flows along the shelf break and slope at intermediate depths (± 100–300 m), except during the late autumn and winter, when it may surface as the Davidson Current (from Point Conception to at least southern Washington). Coastal upwelling, a phenomenon near the coast related to alongshore wind stress, and farther offshore perhaps to positive wind-stress curl and cyclonic eddies, is a dominant process on the shelf during spring and summer. The strength and persistence of upwelling decline in autumn. Upwelled waters are cool, nutrient rich, and relatively saline, particularly at upwelling centres off Cape Mendocino, Point Arena, Point Sur, and Point Conception.

Upwelling is most prominent off Point Conception in late spring, occurring progressively later in the summer at higher latitudes (Bakun and Nelson 1977). At times, upwelled water may occur as plumes extending hundreds of kilometres offshore (Traganza *et al.* 1981). Steep gradients in temperature, nutrient, and biological properties often exist offshore when upwelling plumes intrude into the California Current.

5. Methods

5.1. Phalarope distribution

We counted all phalaropes within 50-m strip transects (determined by inclinometer) along 39 east–west lines surveyed from aircraft during 21–25 September 1981 (Fig. 1). A total of 3182 linear km of aerial trackline was surveyed; lines averaged 76 km in length. Transect lines were surveyed from 65-m altitude at an airspeed of 165 km/h. Two observers alternated watches while three others recorded data. Observations were recorded orally on tape; location of each bird sighting (to ± 0.1′ latitude/longitude or approximately 0.2 km) was determined with an onboard VLF navigational computer. Transcribed data were computer-processed for density analysis by location.

While travelling at 15–18 km/h aboard a research vessel along three transects on 24 and 26 September and 3 October, we recorded all phalaropes seen within 400 m to either side (Fig. 2). Two observers were located 4 m above the water. Our shipboard observation techniques and a comparison of ship and aerial survey procedures appear in Briggs, Lewis *et al.* (1981) and Briggs and Hunt (1981).

Bird behaviour was classified according to activity at first sighting (fly, swim, feed), direction of travel, associations with other organisms or physical features like slicks, flotsam, and water-colour boundaries. Feeding by phalaropes could not be discerned from the air.

5.2. Phalarope diet

We collected 58 phalaropes along the ship tracks; 53 were Red Phalaropes and five were Red-necked Phalaropes (*Phalaropus lobatus*). Birds were tagged and frozen immediately upon retrieval. Many soft-bodied prey were subsequently identified from the stomachs, so immediate freezing of specimens appears to have minimized digestion. We recorded standard measurements of the birds after thawing. Proventriculi and ventriculi were removed intact, weighed, bound in cheesecloth, fixed in buffered Formalin, and after 24 h were transferred to 40% isopropyl alcohol.

The wet weights (to nearest 0.01 g) of gut contents were measured separately after sieving through 60 or 80 mesh screens; items as small as 0.3 mm were retained on the screens. It is unlikely that phalaropes prey on organisms smaller than this. Frequency of occurrence and percent volume of each identifiable item, and the minimum number of whole prey were determined for each stomach. When possible, all crustaceans were identified to species; other taxa were identified to family or order.

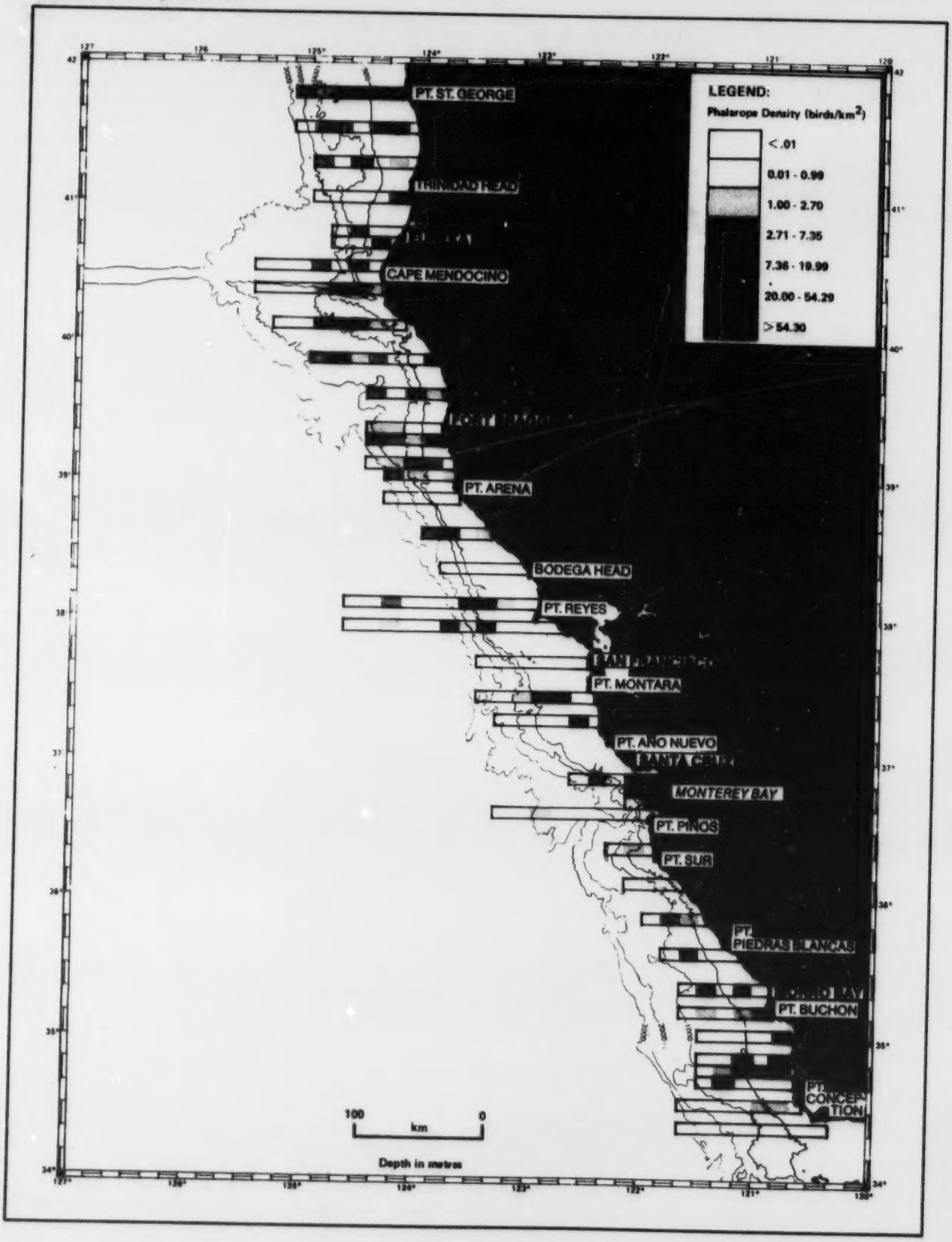
5.3. Plankton

To assess the relative composition and availability of potential planktonic prey, we made 17 oblique and 2 surface plankton tows as the ship travelled at 3–5 km/h with a 1-m-diameter net of 1-mm mesh. Oblique hauls were from approximately 40 m to the surface; a flowmeter attached to the net bridle estimated the volume of water filtered. Sampling occurred at 7–10-km intervals along ship tracks and wherever phalaropes were collected for diet analysis; waters within and on either side of moderate thermal fronts were sampled on each line as were several slicks. Samples were preserved in 10% buffered Formalin. Lab analyses of replicate subsamples from each haul included frequency of occurrence and size determinations for all major macrozooplankton taxa and enumerations of all crustacean species.

Most small zooplankton and highly motile fish larvae may have been missed at the towing speed and mesh we used, but less motile organisms in the size ranges likely to be exploited by phalaropes were probably included.

Chlorophyll *a* (Chl *a*) concentrations (an estimate of phytoplankton stocks) were measured to approximately one-third photic depth along aircraft tracklines with a differential radiometer (Arveson *et al.* 1973). Simultaneously, the photic zone chlorophyll field was measured throughout the study area by the Coastal Zone Color Scanner Satellite. Surface chlorophyll concentrations were

Figure 1
Phalarope density along aerial survey lines in central and northern California, 21–25 September 1981



measured along ship tracks by use of a flow-through fluorometer (Lorenzen 1966). Comparison of these data permitted calibration of synchronous satellite and aircraft chlorophyll values and interpolation of chlorophyll isopleths between aircraft tracklines.

5.4. Hydrographic measurements

Sea surface temperature (SST) was measured along aircraft transects with a precision radiation thermometer (accurate to ±0.2°C) coupled to a chart recorder. The entire coastal and offshore SST field was mapped at thermal infrared wavelengths (10.5–12.5 μm) on 22 September from the NOAA-6 satellite.

Along ship tracks, SST was measured continuously by a through-hull thermometer, and vertical temperature profiles were made at 20 sampling stations using 0–200 m expendable bathythermographs, 0–30 m CTD (conductivity–temperature–depth) casts, or both. Salinity was measured at the surface at 20 stations and at depths of 0–30 m at 11 stations to determine seawater density sections.

Surface concentrations of NO_3-N and PO_4-P were measured spectrophotometrically from 20 filtered samples. Nutrient concentrations and ratios provide important clues to the relative recency of nutrient regeneration from upwelling (Traganza *et al.* 1981).

6. Results

6.1. Phalarope distribution in relation to habitat

A total of 1573 phalaropes was seen in 297 sightings of 1–65 individuals during the aerial survey. Birds occurred within transects as far offshore as 115 km off Point Reyes (Fig. 1), and outside transect lines ("off transect" sightings) out to 195 km, also off Point Reyes. Phalaropes were concentrated just seaward of the shelf break and were less numerous closer to and farther from shore: 46.4% of all individuals and 48.4% of all sightings occurred in waters of the central slope (600–2000 m) although only 20.9% of survey effort was expended in waters of this depth range. By comparison, 30.0% of effort was directed into shelf waters (0–200 m), yielding 27.7 and 27.3% of individuals and sightings, respectively, while the 20.8% of effort expended in waters exceeding 2000 m resulted in only 2.8% of the individuals seen and 5.7% of the sightings. The heavily populated central slope area lies at distances ranging from 10 to 75 km offshore, averaging about 35 km.

Phalarope densities were high (exceeding 54.3 birds/km^2) in 13 aerial transect segments (10′ of longitude); four of these were located over the shelf and nine over the slope. Red-necked Phalaropes comprised 5–10% of all phalaropes seen during ship surveys in the Point Reyes–Monterey Bay sector; the rest were Red Phalaropes. The high numbers of birds observed over the shelf south of Point Buchon may have been predominantly Red-necked Phalaropes, because migration of that species tends to occur closer to shore than does that of Red Phalaropes (Briggs, Chu *et al.* 1981). We observed a similar distributional pattern during September–October 1980 (unpubl. data).

Because most phalaropes occurred in waters of intermediate distance from shore and of intermediate depth (median water depth of all phalarope sightings was 223 m), phalarope density was not significantly correlated with distance to shore or water depth (distance: Pearson's $r = -0.05$, $p = 0.20$; water depth: $r = -0.10$, $p = 0.07$; $N = 399$ 5′ × 5′ [latitude–longitude] "grid cells" for which density and physical parameters were measured). Further, phalarope density was not related linearly to surface temperature *per se*; the great majority of sightings occurred at intermediate values within the 10.0–18.0°C range that we sampled.

In contrast, most phalarope sightings occurred in areas of moderate to strong surface thermal gradients (>0.08°C/km). Figure 3 compares the strength of thermal gradients in 158 grid cells having phalarope sightings with

Figure 2
Details of sea-surface-temperature (SST) field off central California on 22–23 September 1981. Isotherms between aerial survey lines (shown on Fig. 1) are from NOAA-6 satellite images. Dashed lines indicate ship coverage on 24 (top line) and 26 (middle line) September and 3 October (bottom line)

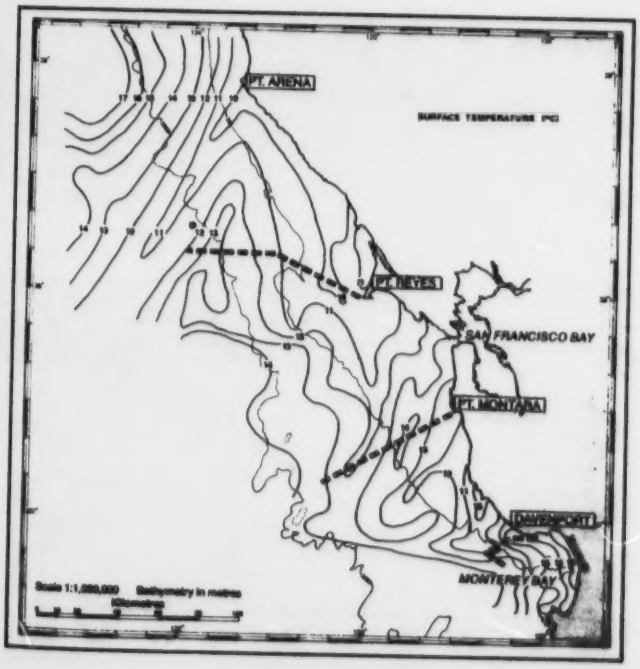
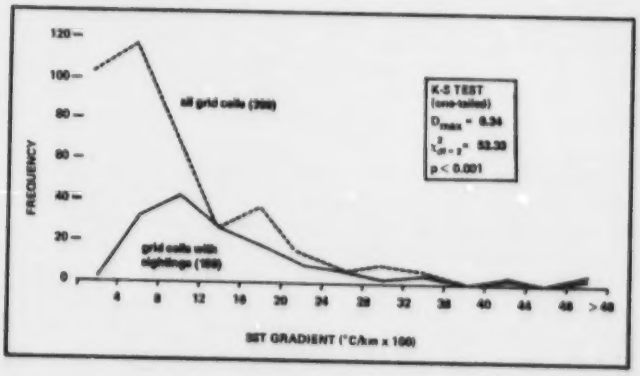


Figure 3
Frequency distributions of SST gradients in 5′ × 5′ latitude/longitude grid cells having phalarope sightings compared with SST in all grid cells. Data are from aerial surveys conducted during 21–25 September 1981. Kolmogarov-Smirnov test of goodness-of-fit shows that phalarope sightings were significantly concentrated in the grid cells having moderate to strong SST gradients



the strength of thermal gradients in the 399 grid cells surveyed. (Since bird distribution may relate to temperature gradients between surveyed lines as well as to gradients on lines, we interpolated the shape of isotherms between lines using coincident satellite infra-red (IR) imagery and assigned temperatures to ±0.5°C by comparing satellite data with simultaneous airborne radiometer data taken on adjacent transect lines.) Thermal gradients in grid cells having phalarope sightings were significantly stronger than would be expected by chance ($p<0.001$, $\chi^2_{df=2} = 52.33$).

Steep gradients in SST occurred primarily at the boundaries between waters upwelled on the shelf and the adjacent waters of the California Current. Several very strong SST gradients were seen 100–250 km offshore in satellite IR images. Phalaropes were not especially numerous on either side of SST fronts. Instead they concentrated where SST changed rapidly with horizontal distance.

Phalarope sightings were concentrated to a significant degree in waters of low chlorophyll; grid cells with phalaropes averaged 0.19 mg Chl *a*/m^3 whereas all cells averaged 0.41 mg/m^3 (one-tailed K-S test of goodness-of-fit comparing frequency distributions of chlorophyll [determined by airborne radiometer] in grid cells having phalaropes with chlorophyll in all grid cells; $D_{max} = 0.257 + \chi^2_{df=2} = 33.21$; $p<0.001$). Where Chlorophyll *a* was most concentrated (3–8 mg/m^3 very near the coast), phalaropes were relatively scarce.

Birds offshore (60 sightings of 329 birds >65 km from land), occurred in waters with a narrow temperature range, averaging slightly cooler than the mean of offshore grid cells (birds: range 11.1–16.2°C, $\bar{X} = 12.3 \pm 1.3$°C [SD] versus grid cells: range 11.1–17.4°C, $\bar{X} = 12.9$°). Phalaropes frequented offshore waters where SST gradients were strong ($X_{birds} = 0.14$°C/km *vs* $X_{grid\ cells} = 0.04$°C/km) and where chlorophyll concentrations were low ($X = 0.08$ mg Chl *a*/m^3 in cells where birds occurred).

6.2. Environmental cues for feeding

To determine the importance of visible environmental cues to foraging phalaropes, we analysed sightings of feeding flocks observed from the ship and sightings of stationary flocks (not flying) seen from the airplane. All but 66 of 500 phalaropes seen from shipboard on 24–26 September occurred in flocks feeding at slicks, as did all but about 20 of approximately 2500 seen on 3 October; no feeding flocks were seen away from slicks. Eighty-six percent of all birds seen during aerial surveys occurred in flocks (>3 birds); stationary flocks accounted for 669 birds (49.9% of the flock total). Of these, 442 phalaropes occurred in 62 stationary flocks at surface cues including slicks; colour boundaries; lines of flotsam, kelp, or foam; concentrations of baitfish; and swarms of plankton (Table 1). (The remaining phalaropes in stationary flocks may have been associated with surface cues that we failed to note due to glare, rough seas, and other conditions affecting aerial sightings.) These environmental cues are much less extensive than the thermal gradients discussed above (tens of metres to a few kilometres versus one to tens of kilometres) and all but three of the surface cues were located within strong or moderate SST gradients (>0.15°C/km or 0.08–0.15°C/km, respectively). Further, except for eight flocks comprising 64 birds, all other phalaropes in flocks (both flying and stationary) occurred within strong or moderate SST gradients. Eight of 41 discontinuities had no phalaropes; six of the eight were within 4 km of the coast and resulted from differences in suspended sediment between adjacent parcels of water, not from differences in chlorophyll concentration.

6.3. Phalarope feeding in central California upwelling systems

Phalarope feeding in relation to upwelling systems of different structure, dynamics, and apparent secondary productivity was examined from shipboard off central California. Because the development of upwelling conditions differed with area and time from 24 September through 3 October, each area is discussed separately.

6.3.1. *24 September — Point Reyes* — The 90-km ship track surveyed off Point Reyes extended into waters deeper than 3000 m. Northwest winds of 45–60 km/h during this and the preceding 3 days led to very active upwelling over the shelf. Isopyenals were upturned sharply toward the coast; the seasonal pycnocline (25.5 σT) surfaced at about 60 km offshore (Fig. 4) and coincided with a 1°C temperature gradient (0.2°C/km^2). This surface density front was within an area of elevated surface-chlorophyll concentration located 10-km seaward of a modest chlorophyll gradient (Fig. 5). The NO_3:PO_4 ratio declined from the area of the shelf seaward to the front, indicating transition from newly upwelled to more oceanic waters.

Phalaropes were found from about 47–79 km offshore, peaking in abundance at the front (Fig. 5). Thirty percent of 318 phalaropes seen were identified as reds; the rest were unidentified. Flocks totalling 106 birds visited slicks near the front. Ten Red Phalaropes, collected from flocks feeding near the front, recently had fed on euphausiids, including *Euphausia pacifica*; euphausiids totalled 47% of proventricular prey volume and 38% of prey numbers. Unidentified crustacean parts accounted for an additional 10% of volume. Other crustacean groups and plastic particles were less prominent. In contrast, fish eggs of two species (King-of-the-salmon, *Trachipterus altivelis* and Medusafish, *Ichichthys lockingtoni*), accounted for two-thirds of ventricular prey volume, whereas euphausiids comprised about a tenth. Barnacle cypris larvae, euphausiids, fish eggs, sand, and plastic each were contained in at least half of the stomachs (Table 2).

Prey items ranged in size from gastropod veliger and barnacle cypris larvae averaging 1.3–1.6 mm and 2.0 mm in length, respectively, to a 4-mm specimen of *Calanus* sp.,

Table 1
Presence of phalaropes at surface discontinuites indicative of convergences. Aerial sightings were on 21–25 September 1981

Type of discontinuity ("cues")	No. of discontinuities with (without) phalaropes	No. of birds (flocks) seen	Range of SST gradient*
A. Slicks (lacking floating material)	6 (1)	54 (11)	0.27 – 0.54
B. Slicks with kelp, foam, or flotsam	11 (0)	259 (26)	0.10 – 0.27
C. Colour boundaries	14 (7)	118 (22)	0.09 – 0.54
D. Plankton and baitfish swarms	2 (0)	11 (3)	0.18

*SST gradient in °C/km within 5′ latitude-longitude grid cell in which sighting occurred.

and 11–16 mm euphausiids. Fish eggs ranged in size from 1 to 4 mm.

Herbivorous salps (*Dolioletta* sp.) and carnivorous siphonophores together comprised 80–95% of zooplankton numbers and volume in plankton tows inshore of the front (stations 1–4). The dominant crustaceans were *Eucalanus californicus* and *Euphausia pacifica* (Table 3). Numbers of crustaceans (particularly *Calanus pacificus*) were higher in tows made at the slicks where feeding phalaropes were collected (stations 5 and 6), while *Dolioletta* sp. and siphonophores remained common (1–4 individuals/m^3). Fish eggs, so prominent within phalarope ventricular contents were quite rare in the tows, and barnacle cypris larvae (which accounted for 4% of prey volume and 36% of animal prey numbers) were completely absent. Both phalarope and *Calanus* (though not overall crustacean) abundance peaked at the front (Table 3 and Figure 5).

Table 2
Contents of the stomachs of 10 Red Phalaropes collected on 24 September off Point Reyes. Data from proventriculi and ventriculi are combined

Item	No. stomachs with item	Minimum no. whole prey	% of prey volume
Hydrozoan sp.	2	2	0.1
Gastropod sp.	5	7	0.2
Gastropod veliger	2	2	0.1
Crustacean parts	1	—	0.8
Cirriped cypris	6	230	4.0
Calanus sp.	1	1	0.1
Brachyuran zoea	1	1	0.1
Euphausiid sp.	2	6	2.1
Euphausia pacifica	5	44	28.0
Insect parts	4	—	2.2
Fish eggs	8	349	59.0
Sand grains	6	—	0.1
Plastic particles	6	—	1.1

6.3.2. *26 September — Point Montara* — Hydrographic conditions along a trackline to 80 km off Point Montara into waters 2750 m deep, changed considerably from 23 to 26 September. Measurements of SSTs from the airplane on the 23rd revealed a tongue of cool water extending from Point Reyes, intersecting the ship trackline between 40 and 70 km off Point Montara (Figs. 2 and 6). Southerly winds of 25–35 km/h on the 24th resulted in general warming of surface waters. Subsurface isotherms were only slightly upturned near shore on the 26th and SSTs offshore were 2.0+ °C warmer than when measured from the air. Offshore waters were now thermally stratified to 50 m (density sections at offshore stations showed similar stratification). Chlorophyll *a* was most concentrated within 20 km of the shore, was lowest from 40 to 60 km out and rose to 1–2 mg/m^3 farther offshore (Fig. 6). Nutrient concentrations were lower than off Point Reyes; ratios of NO_3:PO_4 were intermediate between upwelled and oceanic waters.

One hundred eighty-two phalaropes were seen along the ship track, despite the presence of dense fog for the first 20 km (airborne observers saw no phalaropes within this inshore zone on 22 September). Only 4% of the birds seen were identified to species and all were reds. Phalaropes were most numerous between 70 and 80 km from shore, with

Figure 4
Surface-layer density (σ_t) section for Point Reyes transect, 24 September 1981

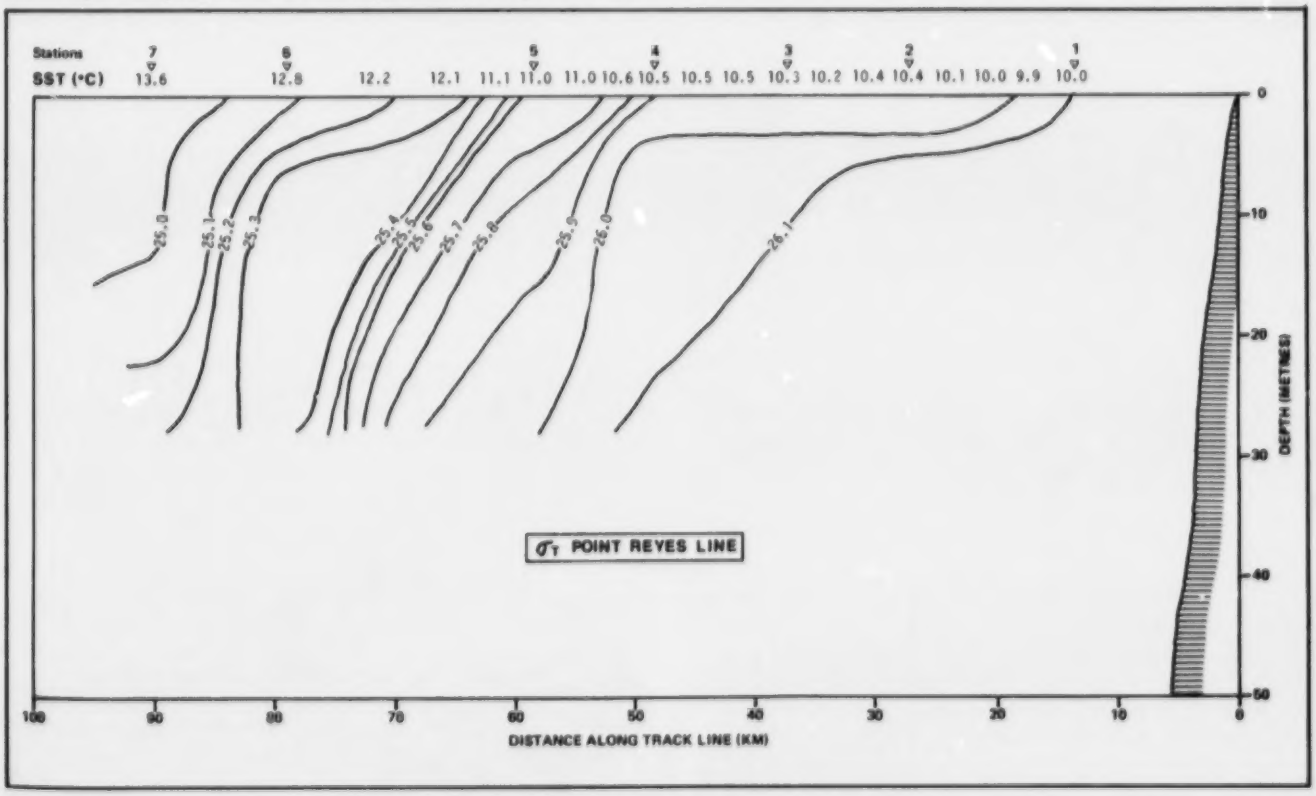


Table 3
Density (number · m^{-3}) of crustaceans, ichthyoplankton, and other macrozooplankton collected in 17 oblique and 2 surface (stations 14B and 19) tows on 24 and 26 September and 3 October, off Point Reyes, Point Montara, and Davenport, respectively (P indicates present in densities less than 0.1 m^{-3})

	Point Reyes transect							Point Montara transect										Davenport transect	
Station	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14A**	**14B**	**15**	**16**	**18**	**19**
(km from coast)	**(14)**	**(27)**	**(37)**	**(48)**	**(58)**	**(78)**	**(91)**	**(11)**	**(19)**	**(29)**	**(38)**	**(45)**	**(52)**	**(59)**	**(59)**	**(68)**	**(78)**	**(19)**	**(28)**
Taxon																			
Crustacean larvae	—	—	—	—	—	—	—	—	—	1.0	1.6	0.3	0.2	P	—	0.5	0.1	0.9	0.7
Copepoda																			
Cyclopoida	—	—	—	—	P	P	P	—	—	—	—	—	—	—	—	—	—	—	—
Calanus pacificus	0.5	0.2	P	—	1.3	0.9	0.2	0.4	0.4	1.0	9.3	0.7	7.1	7.4	1.9	1.6	5.4	118.2	13.4
Eucalanus californicus	P	0.2	0.7	0.9	0.9	0.9	0.7	3.7	1.2	—	1.3	1.7	2.8	—	—	0.2	0.6	—	—
Euphausiacea																			
postlarvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13.8	—
Euphausia pacifica	P	—	1.9	P	—	0.3	0.1	0.3	0.5	10.4	0.1	5.5	2.5	0.5	—	P	0.4	0.3	—
Thysanoessa sp.	P	P	—	P	0.4	0.2	0.1	0.3	0.3	0.2	—	—	—	—	—	—	—	—	—
Mysidae	—	—	—	—	—	—	—	—	—	P	—	—	—	—	—	—	—	—	—
Amphipoda																			
Hyperiidae	P	0.1	P	P	P	0.3	—	—	0.2	0.6	P	—	0.2	0.2	—	P	0.1	P	—
unidentified	—	—	P	—	P	—	0.1	P	—	—	—	—	0.2	—	—	—	—	—	—
Decapoda																			
Porcellinid larvae	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—
Brachyuran larvae	P	0.3	P	—	P	—	—	1.2	0.6	—	—	—	—	—	—	0.2	P	—	—
Fish eggs/larvae	—	—	—	—	—	0.1	—	P	—	P	P	—	—	—	—	—	0.1	—	—
Unidentified egg	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	P	P	—	P	P
All other zooplankton*	0.7	3.0	69.9	5.4	2.6	8.1	4.9	3.3	2.7	42.6	19.2	4.5	16.0	15.3	0.6	2.8	3.1	0.1	2.0
Total crustacean density	0.6	0.8	2.5	1.0	2.6	2.7	1.3	6.0	3.2	13.2	12.8	8.2	12.8	7.7	1.9	2.6	6.7	133.2	14.3
Total zooplankton density	1.3	3.8	72.6	6.3	5.2	10.9	6.2	9.3	5.9	55.8	32.0	12.7	28.9	23.0	2.5	5.4	9.8	133.3	16.3
Moulted crustacean carapaces	—	—	—	—	—	—	—	—	—	10.5	—	—	—	—	439+	P	—	4.9	5.1

*Numerically important species included *Dolioletta* sp. (Thaliacia), Leptomedusae and Trachymedusae (Coelenterata: Hydrozoa), Physonectae (Hydrozoa), Cydippida (Ctenophora), and *Sagitta* sp. (Chaetognatha).

only smaller concentrations elsewhere (Fig. 6). Most birds were flying through this area; only three feeding flocks were seen, all near slicks at stations between 50 and 72 km offshore.

Six Red Phalaropes were collected from flocks in slicks at 59 and 72 km from shore. The foreguts of two birds were empty, suggesting that they had not fed recently. The foreguts of the other four birds contained primarily euphausiid parts, plus two whole *Thysanoessa spinifera* (Table 4). The hindguts of all six birds contained primarily fish eggs (accounting for 38.6% of total prey volume) and euphausiids. Euphausiids were well preserved, indicating that they were eaten recently. The sizes of prey taken by these birds were similar to those taken by birds off Point Reyes.

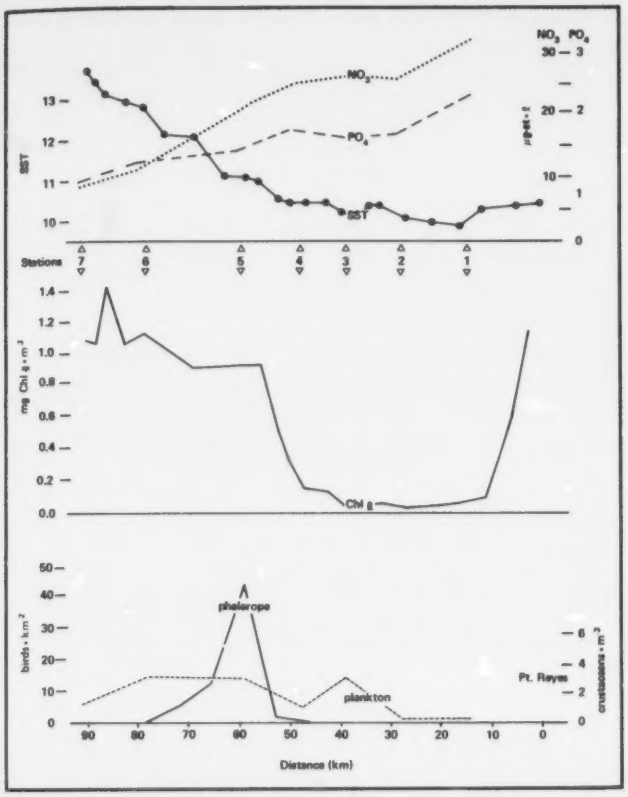
As was seen in plankton tows off Point Reyes various medusae and *Dolioletta* dominated both numbers and volume at stations out to 50 km; their abundance declined farther offshore. Crustacean density averaged much higher all along this track than off Point Reyes, owing to sizable populations of *Euphausia* and *Calanus* inshore and of *Calanus* beyond 50 km (Table 3). The phalarope flock at station 14, from which four birds were collected, was apparently attracted to extremely dense concentrations of moulted calanoid carapaces and moderate surface concentrations of live *C. pacificus*; subsurface *C. pacificus* density at station 14 was the highest encountered on this track. Small numbers of amphipods occurred all along the line while larval crustaceans were common at stations 10, 11, and 15. Euphausiids from Point Montara to station 13 were considerably larger than those farther offshore.

6.3.3. *3 October — Davenport* — Waters near the southern edge of a small upwelling plume extending southwest from Point Año Neuvo were sampled during a period of light northerly winds following the storm of the previous week. Aerial and satellite SST data taken before the storm showed intense upwelling; SSTs as low as 10°C occurred near shore (Fig. 2). Only weak upwelling was evident on this 30-km ship track on 3 October (Fig. 7), with Chlorophyll *a* and nutrient conditions much like the shelf-break section of the Point Montara transect (stations 9 and 10). Satellite images from late September through early October, consistently showed this region to be a zone of intermixing of waters upwelled to the north with warmer, oceanic waters from west of Monterey Bay.

We collected 42 phalaropes from among approximately 2500 birds in several flocks at a 0.8°C thermal front (0.14°C/km) just seaward of the shelf break. Though no direct counts of species proportions were made here, 5 of the 42 specimens collected were Red-necked Phalaropes, while the rest were reds.

In contrast to the gut contents of birds collected elsewhere, these birds had fed to a great degree (53% volume) on *Calanus* sp. (Table 5) with lesser amounts of

Figure 5
Comparison of temperature (in degrees Celsius), nutrients, and plant and animal populations at sampling stations along Point Reyes ship tract, 24 September 1981. The seasonal pycnocline (25.5 σt) surfaced near 60 km



brachyuran larvae, euphausiids and other crustaceans. Insect parts (Coleoptera) were found in about one-third of all ventriculi, and about half contained large numbers of crustacean zoea and nauplii (0.5 mm to about 1.5 mm).

Surface and oblique zooplankton tows demonstrated the extreme numerical predominance of *Calanus* among crustaceans here (Table 3). One-third of all phalaropes collected on this date were taken on a slick at station 18 where surface swarms of *Calanus* were ubiquitous. The presence at station 19 of euphausiid carapaces — indicative of active growth and moult — is noteworthy, in view of the 13% contribution this group made to proventricular prey volume. Substantial numbers of crustacean larvae were taken in plankton tows here. Clearly, conditions had been favourable for crustacean moult for some time off Davenport and perhaps also to the north, where reproductive products may have originated before drifting south.

7. Discussion

In light of recent studies of plankton ecology in upwelling regions and Brown's (1980) concept of phalarope's dependence upon physical concentrating mechanisms for successful feeding, several inferences can be drawn from our California Current data:

1. Nutrient regeneration through upwelling enhances plant production and growth, leading to relatively high standing stocks of herbivorous zooplankton. Vertically migrating zooplankton may remain in the same general location relative to the source of upwelling by alternately migrating to strata having opposite mean currents (Smith *et al.* 1981*a*, Smith *et al.* 1981*b*), but they tend to accumulate at offshore convergences because of rapid advection within the Ekman layer (~0–30 m; Huyer 1976).

a. Phalaropes feeding in convergences should encounter relatively high prey availability;

b. Foraging phalaropes should utilize visable environmental cues to locate convergences;

c. Off California, feeding flocks should be common in thermal fronts where upwelling waters converge with surface waters of the California Current;

d. Because nutrient and chlorophyll concentrations may be highest near the source of upwelling, phalarope distribution should not necessarily exhibit a positive correlation with either;

2. Unless dispersed by extreme turbulent mixing due to wind, the zooplankton found near fronts are distributed in patches (Holligan 1981, Husby and Nelson 1981). Phalarope feeding success along a convergent front may therefore be quite variable and bird occupation of such a feature should be patchy;

Table 4
Contents of the stomachs of six Red Phalaropes collected on 26 September off Point Montara. Data from proventriculi and ventriculi are combined

Item	No. of stomachs with item	Minimum no. whole prey	% of prey volume
Hydrozoan sp.	1	1	0.6
Cirriped cypris	4	13	1.8
Hyperiid amphipod	2	22	1.0
Euphausiid parts	3	3	13.0
Euphausia pacifica	1	7	13.6
Thysanoessa longipes	2	8	14.4
Thysanoessa spinifera	1	2	13.1
Insect parts	2	2	1.6
Fish eggs	6	577	38.6
Sand grains	2	—	2.2
Plastic particles	3	—	0.1

Table 5
Contents of the stomachs of 37 Red Phalaropes and 5 Red-necked Phalaropes collected on 3 October 1981 off Davenport. Data from proventriculi and ventriculi are combined*

Item	No. of stomachs with item	Minimum no. whole prey	% of prey volume
Hydrozoan sp.	2	6	0.1
Thecate hydrozoan	1	1	<0.1
Gastropod sp.	2	5	<0.1
Pteropod sp.	1	1	<0.1
Crustacean parts	3	—	11.2
Crustacean larvae	23	4056	5.8
Cirriped cypris	9	14	1.0
Calanus sp.	39	3923	52.8
Brachyuran larvae	36	516	5.0
Euphausiid sp.	8	80	4.4
Euphausiid larvae	10	167	2.0
Euphausia pacifica	2	2	0.2
Thysanoessa Spinifera	2	2	2.6
Insect parts	7	—	4.8
Coleoptera sp.	11	35	1.6
Halipid coleopteran	1	1	<0.1
Fish eggs	17	28	0.8
Sand grains	5	—	<0.1
Plastic particles	25	—	4.0
Seeds	2	2	0.1
Unidentifiable material	16	—	4.6

*One trematode (<0.1% total volume) was found; it was unknown whether it was parasitic on the bird.

3. Captive phalaropes prefer large prey (9–18 mm) but concentrate their feeding on smaller (1–4 mm), less motile organisms (Dodson and Egger 1980). Within these constraints, where the species composition of appropriately-sized prey differs between the upwelling source waters and the frontal zone, phalarope diet should reflect species composition of the latter.

Our study occurred during the peak of fall migration when phalaropes were among the most numerous seabirds throughout a broad (200-km) section of California coastal waters. Despite their abundance and wide distribution we found that phalarope feeding flocks (including stationary flocks seen from the airplane) were virtually restricted to areas having strong surface thermal gradients, especially where slicks and other discontinuities were also present. Thus, our findings bear directly on some of the above hypotheses and suggest refinements in methodology that in the future may be used to clarify additional relationships.

7.1. Oceanographic conditions and phalarope abundance

Like the data reported by Orr *et al.* (1982) for arctic Canada, our aerial survey showed that phalaropes were most numerous over the continental slope. The studies of Bakun and Nelson (1977), Traganza *et al.* (1981), and Breaker and Gilliland (1981) confirm that waters upwelled on the California shelf typically interact with California Current surface waters over or seaward of the slope. Using a 21-year California Cooperative Oceanic Fisheries Investigations (CalCOFI) time series, Bernal and McGowan (1981) found that off San Francisco, peak spring–summer zooplankton biomass occurred seaward of the shelf, at 150–180 km from shore. Though we did not sample plankton at that distance off San Francisco, we did observe phalaropes at a 5–7°C thermal front about 160-km offshore. This front marked the seaward boundary of a plume of cold water contiguous with the intense upwelling we sampled off Point Reyes. Previous observations of phalarope occurrence during migration and winter stressed the importance of *upwelling centres* (Murphy 1936, Höhn 1965, Ashmole 1971), but the present data suggest that waters near upwelling centres are relatively less important to feeding phalaropes than convergences farther offshore. In this respect our data resemble those of Brown (1979), though the physical mechanisms he observed off Senegal differ markedly in scale and duration from those off California.

As postulated above, phalaropes occurred at visible indications of convergence: two-thirds of stationary flocks observed from the air were on slicks, colour boundaries, and so on; almost all other flocks were in moderate or strong SST gradients. Additionally, all stationary and feeding flocks observed from the ship were at slicks. Similarly, phalaropes were observed from the air at all but eight of 41 surface discontinuities; six of the unpopulated colour boundaries resulted from turbid waters close to shore, a situation which might repel rather than attract the birds. Because most thermal fronts and visible discontinuities sampled by us were roughly parallel to the coast, our tracklines crossed them perpendicularly. Hence, our data do not directly bear on the question of phalarope flock distribution *along* fronts. However, occurrence of flocks at almost all offshore discontinuities encountered suggests that phalarope flocks occurred along very sizable sections of these features. The relationships between zooplankton patchiness and flock distribution along fronts may best be assessed by sampling within and parallel to fronts and perhaps by sampling through time at fixed sites (Magnuson *et al.* 1981).

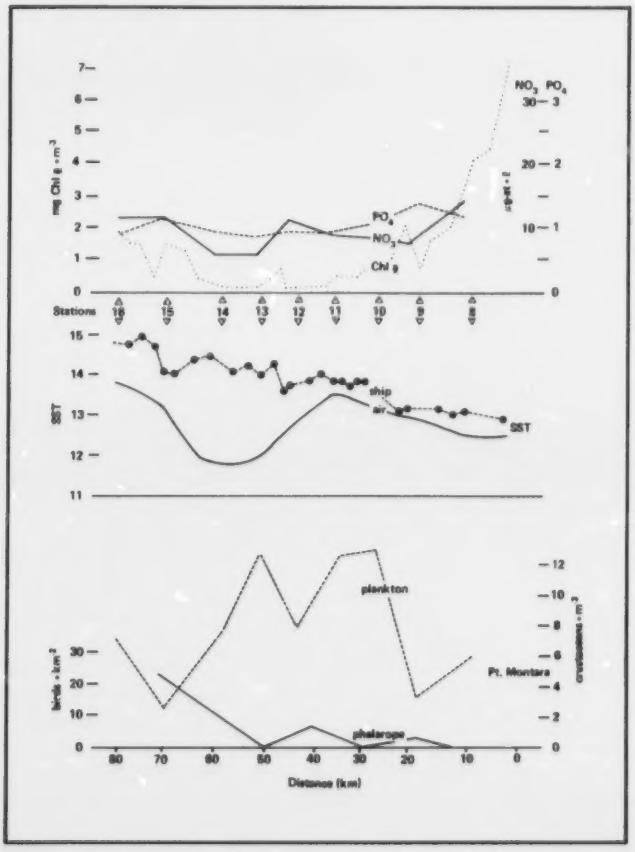
Phalarope numbers varied independently of concentrations of nutrients and inversely with chlorophyll. Predominance of birds in waters of low chlorophyll (generally <0.08 mg/m^3) corresponds to the spatial separation of high herbivore populations (upon which phalaropes feed) from the highest standing stocks of plants (Walsh 1976, Peterson *et al.* 1979).

7.2. Phalarope diet and prey availability

The substantial variety of crustaceans, insects, and inanimate items consumed by the birds we collected (Tables 2, 4, and 5) indicates that phalaropes are rather non-selective in their feeding although, except for fish eggs, gelatinous prey were not often consumed. Except for euphausiids of 11–16 mm found in birds collected off Point Reyes and Point Montara, the size ranges of prey we measured (0.3–8.0 mm) correspond closely to the sizes of prey selected by phalaropes during the experiments of Dodson and Egger (1980).

Our oblique tows demonstrated that several species of zooplankton (especially *Eucalanus*) were abundant but

Figure 6
Comparison of temperature (in degrees Celsius), nutrients, and plant and animal populations along the Point Montara ship tract, 26 September 1981. The cool plume extending south of Point Reyes is shown in aerial SST data for 23 September



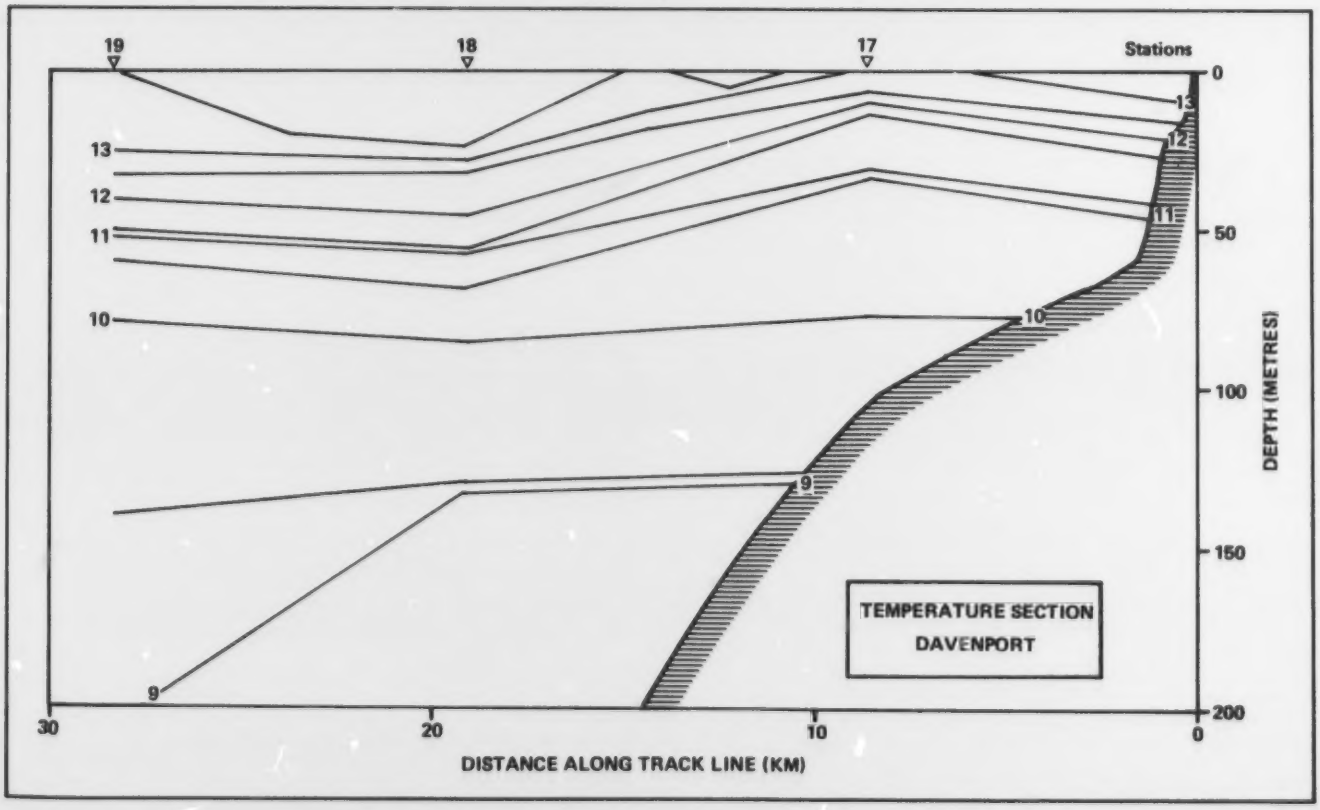
apparently unavailable to phalaropes, probably because these crustaceans stayed below the range of surface-feeding birds. Surprisingly, many euphausiids, including large and motile adults, were eaten by phalaropes, though the adults were poorly represented in tows. Low catches of adult *Euphausia* were probably due to avoidance of our net (with a bridle partially obscuring the mouth). Further, except in highly productive, nearshore waters (Youngbluth 1976), adult *Euphausia* exhibit distinct diurnal vertical migrations and are abundant in surface layers only at night (Brinton 1976). Feeding upon large euphausiids at night or at dawn, just before the prey descended for the day, might account for presence of these items in the birds' diet. Quantitative, day–night sampling of plankton at discrete depths, carried out where phalaropes feed, may resolve this question.

In waters off California during summer, *Calanus pacificus* is among the most numerous of all crustaceans at the surface (Fleminger 1964, Longhurst 1967). Advection of phytoplankton and of the primarily herbivorous *Calanus* away from upwelling centres could account for large *Calanus* concentrations in offshore convergences (Longhurst 1967, Peterson *et al.* 1979). Phalaropes collected off Point Reyes and Point Montara had not fed on *Calanus*; these copepods were not numerous off Point Reyes except seaward of the density front, but substantial subsurface populations were found off Point Montara. It appears that the intensity of advection on the northern line had simply swept surface-dwelling organisms seaward. Plant populations either had not built up to high levels or were concentrated at depth; correspondingly, copepods were scarce at the surface. Off Oregon, Peterson *et al.* (1979) found that when winds favourable to upwelling decreased or reversed, plant and copepod populations rapidly increased in the area shoreward of the offshore, convergent front (i.e. surface waters moved shoreward bringing rapidly doubling plant cells into high-nutrient waters). This "relaxed" situation may have led to the high subsurface crustacean populations off Point Montara. The overwhelming predominance of *Calanus* in birds collected off Davenport clearly reflected the great local abundance of these copepods and their surface swarming in an area of weak convergence.

8. Conclusion

This study supports the idea that phalaropes depend substantially on surface convergences to make their prey available. To reconcile all of the data, however, the additional complexities of (*a*) stability of recent hydrographic conditions and (*b*) proximity to upwelling centres must be integrated. The best possible feeding conditions might be encountered downstream from an active, stable upwelling centre, where plant populations have achieved high standing stocks and where herbivores, such as *Calanus*, and omnivores, such as *Euphausia* and *Thysanoessa*, are abundant. A convergence is required to concentrate these zooplankton within dabbling range of the surface. A strong convergence and nutrient upwelling such as we observed off Point Reyes

Figure 7
Temperature (in degrees Celsius) section for Davenport transect, 3 October 1981



does not, in the absence of high grazing plankton populations, lead to successful feeding by phalaropes. Conversely, an area with abundant zooplankton but lacking a convergence (as off Point Montara) will support few birds.

The importance of convergence-feeding by migrating phalaropes depends on the relative stability and dependability of both upwelling and convergences. Occurrence of wind conditions unsuitable to upwelling or periods of extremely strong wind might lead to adverse feeding conditions in extensive portions of the migration pathway (perhaps 500 km or more). Birds encountering such conditions might starve if they lacked sufficient energy reserves either to wait for better conditions or to pass over the unsuitable region. Bond (1971 and sources cited therein) described a mass mortality of this sort. As yet, the seasonal stability of upwellings and associated convergences off California are incompletely known. Hopefully, additional observations of phalaropes associated with coastal upwelling will provide critical data for refining and testing these ideas.

9. Acknowledgements

We thank J. Christmann and S. Davenport, who persevered through difficult ship surveys and K. Reinhard and D. Allison, who kept our aircraft flying so well for thousands of survey-hours. L.C. Breaker of NOAA–NESS and R. Austin of Scripps Institution's VisLab provided invaluable satellite coverage and interpretations. J. Arveson of NASA–Ames Research Facility loaned us a differential radiometer and other equipment while NMFS–Tiburon Lab provided an XBT recorder. Oceanographic gear and expertise were made available by M. Silver, P. DuVoll, and D. Garrison. We were assisted in the field by M. Pierson, M. Bonnell, and G. Farrens; T. Dohl provided temperature data and much logistical support. G. Moser kindly identified fish eggs from gut samples. D. Briggs and T. Smith aided us with graphics and C. Hitchman and T. Smith typed several versions of the manuscript. We are grateful for critical reviews by L.C. Breaker, E.W. Chu, R.G.B. Brown, D.G. Ainley, W.G. Pearcy, and G.A. Sanger.

This work was supported by the US Department of Interior, Bureau of Land Management under contract #AA551-CT9-33 to the regents of the University of California. This is a contribution of the Center for Coastal Marine Studies, University of California, Santa Cruz.

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Sooty Shearwaters off California: diet and energy gain

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1. Abstract

Sooty Shearwaters (*Puffinus griseus*) in Monterey Bay and off southern California fed primarily on juvenile rockfish (*Sebastes* spp.) from May through July and on northern anchovies (*Engraulis mordax*) in August and September; market squid (*Loligo opalescens*) and euphausiids were minor components of the diet. The change from rockfish to anchovies coincided with completion of moult and with pre-migratory weight gain and fattening. In May, fat content was only 8% of fresh weight; by September fat had increased to 42%. There was little monthly variation in water content or non-fat body components. A number of factors may enhance pre-migratory fattening off California, including the availability of high-calorie anchovies.

2. Résumé

Les Puffins fuligineux (*Puffinus griseus*) dans la baie de Monterey et au large du sud de la Californie se nourrissaient surtout de jeunes scorpenidés (*Sebastes* spp.) de mai à juillet et d'anchois du nord (*Engraulis mordax*) en août et en septembre. Le calmar commun du Pacifique (*Logigo opalenscens*) et les euphausiides étaient un apport secondaire au régime. Le passage des scorpenidés aux anchois coïncidait avec la fin de la mue ainsi qu'avec le gain de poids et l'engraissement prémigratoires. En mai, la graisse ne constituait que 8 % du poids frais; en septembre, elle était passée à 42 %. Il y avait très peu de variations mensuelles dans la teneur en eau ou dans les composantes corporelles non lipidiques. Un certain nombre de facteurs peuvent favoriser l'engraissement prémigratoire au large de la Californie dont la disponibilité en anchois riches en calories.

3. Introduction

Seabirds, because of their abundance, play an important role in the feeding and energy structure of marine communities (Ainley 1980, Brown 1980), but their actual impact has been hard to estimate. Part of the problem stems from the difficulty and expense of making metabolic measurements on free-ranging animals (Wiens and Scott 1975, Furness 1978, Dunn 1979). Models of seabird energetics lack such essential parameters as the kinds and quantities of food consumed, the efficiency of food-to-fat transfer, and the costs of basic maintenance, growth, reproduction, moult, and migration.

There have been many quantitative studies on seabird foods and feeding — studies on individual species, including shearwaters and other procellariiforms (e.g. Imber 1973, 1976; Brown *et al.* 1981; Ogi, this volume), and on whole communities (e.g. Ashmole and Ashmole 1967, Croxall and Prince 1980, Ainley and Sanger 1979). Work on avian metabolism and fat accumulation, however, has focused on passerines (e.g. Odum and Connell 1956, Blem 1976), game, and waterfowl (e.g. Raveling 1979); studies on seabirds are rare (Johnson and West 1973, Krasnow 1978).

From May through September, Sooty Shearwaters (*Puffinus griseus*) are among the most abundant seabird predators in the California Current system (Chu and Briggs, unpubl. data). They feed in immense flocks, often near shore with other seabirds and marine mammals (Sealy 1973, Hoffman *et al.* 1981). Shearwaters "pursuit dive" from the sea surface or "pursuit plunge" from the air, using their wings and feet to manoeuvre under water; they can dive to at least 5 m (Ashmole 1971; Brown *et al.* 1978, pers. obs.). This study examines diet and physiological condition simultaneously during the non-breeding season and identifies relationships among diet, moult, and pre-migratory fattening.

4. Study area and methods

Data were collected in the Southern California Bight (1975–78) during surveys of marine bird and mammal populations (Briggs *et al.* 1981) and in Monterey Bay (1978–79). Both areas are neritic habitats along the California coast (Fig. 1), characterized by spring–summer upwelling and an abundant coastal fauna (Bolin and Abbott 1963, Frey 1971, Jones 1971, Morejohn *et al.* 1978).

In June and August 1978 and from April through October 1979, 166 Sooty Shearwaters were collected by shotgun from Monterey Bay for analysis of gut contents, moult, and fat. Thirty-seven birds were also collected in southern California from May through September 1977.

4.1. Diet

Each bird was tagged at collection and later weighed, measured, and dissected. If dissection could not be done on the day that birds were collected, the carcasses were refrigerated overnight or frozen; all carcasses were reweighed before further processing.

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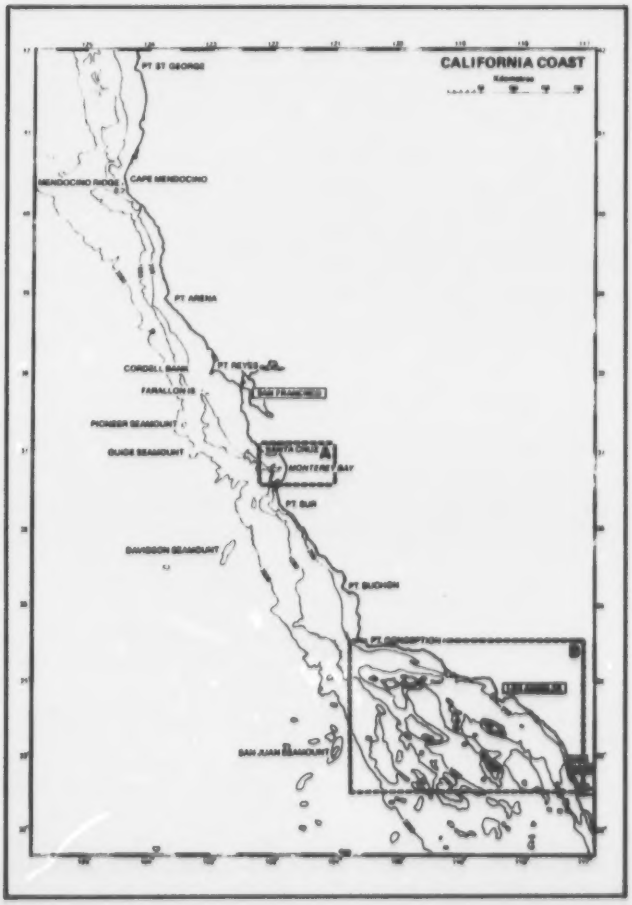
I weighed the contents of the stomachs (including esophagus and proventriculus) and measured food volume by displacement. Gizzard (ventricular) contents, which were fragmented, were not weighed or measured volumetrically. Both stomach and gizzard contents were fixed in 10% buffered Formalin before being separately stored in 40% isopropyl alcohol. The preserved material was later sorted, and prey were identified to the lowest possible taxon; I measured the standard length (SL) (fish), mantle length (squid), or total length (euphausiids) of items whenever possible. I then counted individuals in each prey category and estimated for each bird the percent of total stomach volume represented by each category.

Many of the stomachs were empty, but gizzards often contained prey remains, such as cephalopod beaks and fish otoliths, or other items like pebbles and plastic. Although stomach contents undoubtedly reflect a bird's most recent feeding, it is not known how long remains of previous meals persist in the gizzard. In analysing the data, I therefore analysed stomachs separately from gizzards and whole prey separately from parts of prey.

Figure 1
Coastal California including major submarine topographical features. Sooty Shearwaters were observed and collected in Monterey Bay (A) and in the Southern California Bight (B). Depths in metres



4.2. Weight, moult, and fat content

In 1979, I followed moult progress and fat accumulation in the birds from Monterey Bay. I monitored the progress of moult throughout the season by counting new and growing primary and secondary wing feathers as well as new and growing tail feathers; I estimated the percentage of feathers that were new on other areas of the body. I then divided the number of new primaries plus secondaries by the total number of primaries plus secondaries to give the percentage of completed wing moult for each bird; the percentage of completed tail moult was similarly calculated. For each bird I averaged the figure for completed tail moult with the estimated percentage of completed moult on other body areas (except wings) for an overall percentage of completed body moult. To analyse changes in moult over time, I applied a one-way analysis of variance coupled with Duncan's *a posteriori* multiple range test to monthly mean values for completed moult and for the number of growing feathers.

I determined fat content by measuring visible fat on all specimens and by extracting body fat from a total of 12 birds collected on 25 May, 1 and 22 June, 7 and 31 August, and 21 and 24 September 1979. These birds were prepared for fat extraction by first removing their feathers with large scissors and animal clippers (McLandress 1979). After dissection, the carcasses were refrozen. For all specimens, I measured skin-fat thickness at the anterior and posterior tips of the sternum, and I estimated fat deposits around the viscera on a scale of 1–5 (almost no fat, 1; viscera almost totally obscured by fat, 5). For fat extraction, the 12 shaved carcasses were diced as finely as possible and freeze-dried to constant weight (3–7 days). The dried carcasses were extracted with petroleum ether for 4–5 days in a Soxhlet apparatus, redried under a heat lamp and vacuum for 24–48 h, and weighed again to give total lean dry carcass weight. The extracted fat was similarly dried and weighed. Subtracting lean dry weight from dry weight gave fat content; I used the weight of the extracted fat as a cross-check. For ease of comparison and because lean dry weight is a better indicator of metabolic rate than fresh weight, I have expressed both water and fat content in grams per gram of lean dry weight (Blem 1976).

Since I wished to use measurements of visible fat to predict extractable fat for all the birds collected, I regressed the fat content of extracted birds against each of their skin and perivisceral fat measurements in a stepwise multiple procedure. The best one- and three-variable equations (those giving the highest R^2) follow, where PREDFAT = estimated extractable fat in grams per gram of lean dry weight, SCANT = subcutaneous fat measured at the anterior tip of the sternum, SCPOST = subcutaneous fat measured at the posterior tip of the sternum, and PERI = perivisceral fat index:

$$\text{PREDFAT} = 0.218(\text{SCANT}) - 0.547, R^2 = 0.93, F_{[8]} = 99.11, P = 0.0001 \quad (1)$$

$$\text{PREDFAT} = 0.113(\text{SCANT}) + 0.026(\text{SCPOST}) + 0.169(\text{PERI}) - 0.363$$
$$R^2 = 0.96, F_6 = 49.04, P = 0.0001 \quad (2)$$

I was then able to apply the three-variable model to the larger sample of non-extracted birds. I identified differences in mean monthly weight, water content, and fat and tested them statistically using analysis of variance and

Duncan's multiple range test.

The following expression converted PREDFAT into predicted grams of fat:

$$\frac{\text{Mean PREDFAT}}{1 + \text{mean } H_2O + \text{mean PREDFAT}} \times \text{mean monthly weight} \quad (3)$$

5. Results

5.1. Diet

The diet included 11 genera of fish, seven genera of cephalopods, and at least three genera of crustaceans (Appendix 1). Juvenile rockfish (*Sebastes* spp.), northern anchovy (*Engraulis mordax*), market squid (*Loligo opalescens*), and the euphausiid crustacean *Thysanoessa spinifera* predominated (Table 1), but in both locations diet varied monthly.

5.1.1. *Monterey Bay* — Eighty-seven (57%) of the 154 stomachs examined from Monterey Bay contained food; the rest were either empty or lined with a yellowish mucus. All but one of the gizzards contained identifiable prey parts, and nearly half of them contained small pieces of rigid coloured plastic (*cf.* Baltz and Morejohn 1976).

Fish (especially juvenile rockfish and northern anchovies) were the most important prey among Monterey Bay samples, both by volume and by frequency of occurrence; by number fish ranked second (Table 1). Fish or parts of fish occurred in as many stomachs as gizzards (about 95% of the birds).

By volume, the proportions of rockfish and anchovies were about equal, but anchovies occurred in almost twice as many birds. These two taxa dominated the diet in different months (Fig. 2B): in June, rockfish accounted for 93% of the diet by volume, 36% by number, and occurred in 20 of 23 full stomachs; anchovies first appeared in August when they comprised 90% of the diet by volume and 37% by number and occurred in 18 of 24 full stomachs. The rockfish averaged 70 mm SL; average weight was 5 g. The anchovies averaged 125 mm SL and 24 g in weight.

Cephalopods, primarily squids, were the second most important prey by volume and occurrence (Table 1). Although cephalopods were as common as fish, they only made up 5% of the total volume of stomachs containing food, and although 94% of the gizzards contained cephalopod beaks (as many as 73 sets of market squid beaks in one gizzard), only 36% of the stomachs had squid remains.

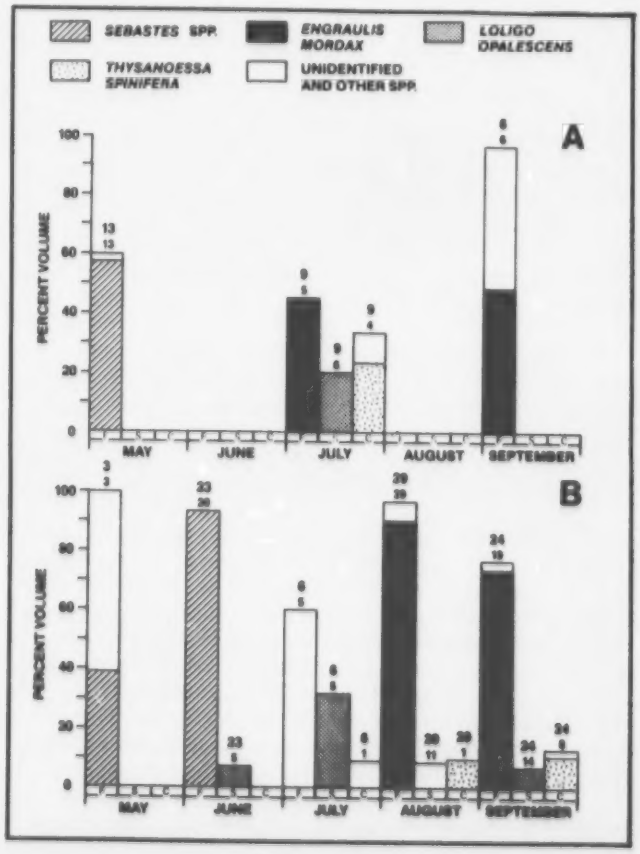
Market squid was the only cephalopod species found nearly whole in stomachs. As determined from regression equations of lower beak dimensions against body measurements, average dorsal mantle length was 109 mm (Kashiwada and Recksiek 1979), and average weight was 20 g (Clarke 1962). Beaks of the octopod *Octopus rubescens* and the squids *Onychoteuthis borealijaponicus* and *Gonatus* spp. occurred regularly in gizzards but rarely in stomachs. Measurements of two intact lower *Gonatus* beaks indicated that the whole animals weighed 48 g and 59 g (Clarke 1962).

Table 1
Major prey of Sooty Shearwaters from Monterey Bay (1978–79) and southern California (1977). Percent occurrence combines data from stomachs and gizzards; percentage volume and percentage number are based on full stomachs only (MBay, Monterey Bay; SoCal, southern California; *N*, number of birds)

	% occurrence		% volume		% number	
	MBay (*N* = 154)	SoCal (*N* = 37)	MBay (*N* = 87)	SoCal (*N* = 29)	MBay (*N* = 87)	SoCal (*N* = 29)
Fish*	97.4	94.6	91	84	33	28
Engraulis mordax	41.6	27.0	44	53	6	1
Sebastes spp.	22.7	62.2	44	17	20	25
Merluccius productus		51.4				
Scorpaenichthys marmoratus		8.1		<1		<1
Cephalopods*	94.8	74.8	5	6	4	2
Loligo opalescens	68.8	35.1	5	6	3	2
Onychoteuthis/ *Gonatus* spp.	47.4	35.1				
Gonatus spp.	40.3	18.9				
Onychoteuthis borealijaponicus	29.2	8.1				
Octopus rubescens	19.5	2.7				
Histioteuthis heteropsis	9.1	2.7				
Crustaceans*	17.5	18.9	3	10	63	70
Thysanoessa spinifera	4.5	10.8	3	7	59	65

*Unidentified and identified material.

Figure 2
Monthly changes in volume of prey in three major categories (F, fish; S, squid; C, crustaceans) found in stomachs of Sooty Shearwaters from southern California (A) and Monterey Bay (B). Numbers above bars represent the number of full stomachs (top) and the number of stomachs containing that prey category (bottom). No birds were collected from southern California in June, and only one bird containing 100% *Engraulis mordax* was collected in August



Euphausiids (*Thysanoessa spinifera* and *Euphausia* sp.), which occurred mainly in September (Fig. 2), were by far the most numerous prey, but their contribution by volume and frequency was small.

5.1.2. *Southern California* — Of 37 gut samples, 29 stomachs (78%) contained food, and eight were empty; altogether 30 gizzards contained identifiable prey parts. Over half contained plastic pieces.

As in Monterey Bay, fish were the most important prey by volume and frequency of occurrence and second by number (Table 1). Fish otoliths were more frequent in gizzards (80%) than were whole fish in stomachs (45%). Of the whole fish, northern anchovies and juvenile rockfish predominated although three birds collected in May contained juvenile cabezon (*Scorpaenichthys marmoratus*). In contrast to Monterey Bay, rockfish occurred more than twice as often as anchovies (primarily in May, and in July as otoliths) but their percent by volume was about one-third that of anchovies. In addition, the rockfish were smaller than those from Monterey Bay, averaging 31 mm SL. Otoliths from juvenile Pacific hake (*Merluccius productus*) were common in May and July samples, but intact animals were not found.

Cephalopod remains were also common, but nearly whole market squid occurred only in six of nine birds in July. Generally, cephalopod remains were less common than fish remains, and they were more common in gizzards (90%) than in full stomachs (45%). Beak fragments from the squids *Onychoteuthis borealijaponicus* and *Gonatus* spp. occurred regularly. Measurements of a whole lower beak from *O. borealijaponicus* indicated a live weight of about 45 g (Clarke 1962).

Euphausiids (*Thysanoessa spinifera*) occurred only in July (Fig. 2A), yet they outnumbered other prey taxa more than two to one. Their overall contribution to the diet by volume was comparable to that of market squid (Table 1).

5.2. Moult

All birds collected in Monterey Bay from May through July wore a mixture of old, new, and growing feathers, but by August, one-fourth of the birds had entirely new plumage; by September, over half the collected specimens had completed their moult. The number of wing and tail feathers in moult was greatest in July (Fig. 3). Wing moult progressed outward from the innermost primary and in both directions from the region of the fourth to sixth secondary; it progressed faster and was completed earlier than body moult. Ogi *et al.* (1981) observed similar patterns among Sooty Shearwaters collected in the northwestern Pacific.

5.3. Body weight, fat, and water content

Except for a 12% decrease in July, mean body weight (weight at collection minus gut contents) increased from May through September (Fig. 4); visible fat also increased. Skin fat thickened from less than 3 mm to 10 mm; it was usually several millimetres thicker at the furcula than over the abdomen and thinnest on the back. Early in the season, perivisceral fat was found only in the mesenteries, but by September it had surrounded the viscera (Fig. 5). The correlation among all the visible fat measurements was high (Pearson $r>0.80$, $P = 0.0001$ for each paired comparison).

Fat — extracted and predicted from equation 2, section 4.2 — also increased from May through September (Fig. 4). The lightest extracted specimen, collected in May, had only 56.8 g of fat, equivalent to 8% of its body weight (corrected for plumage removal). In comparison, the heaviest specimen, collected in September, had 542.9 g or 41% of its body weight in fat. Using a two-way analysis of variance (unbalanced design, Helwig and Council 1979, pp. 242–263) on the data in Fig. 4, I compared the mean values of extracted and predicted fat for each month and also among months (Table 2). Differences between extracted and predicted fat content for each month were not significant, but there were significant differences among months. Duncan's multiple range test (df = 147, alpha = 0.05) revealed no significant differences from May through July, but significantly higher fat content in August and again in September; mean August and September values differed significantly from those of May, June, and July and also from each other. In contrast, there were no statistically significant changes in lean dry weight or water content (Fig. 4).

6. Discussion

6.1. Feeding habits and diet

Most Sooty Shearwater prey in this study either form large surface schools as adults (market squid, anchovies, and euphausiids) or have pelagic schooling juveniles (rockfish, hake, other squids, and *Octopus rubescens*); their distributions off California (Frey 1971, Young 1972, Roper and Young 1975, Anderson 1978) are closely tied to the seasonal distribution of Sooty Shearwaters (Chu and Briggs, unpubl. data). For example, the seasonal abundance of larval rockfish and hake in southern California (Ahlstrom *et al.* 1978, Parrish *et al.* 1981) matches the appearance of juveniles in the diet: the larvae are most abundant in January through March, and juveniles occur in shearwater stomachs April through July. Squids and euphausiids seem to be taken whenever they are available. It is unclear whether deep-water forms whose remains were occasionally present in gizzards, (e.g. *Histioteuthis heteropsis* and *Vampyroteuthis infernalis*) were actively preyed on or scavenged from the surface. These species may have been the prey of some other animal(s) subsequently eaten by the birds. Moreover, there are more cephalopod beaks in gizzards than cephalopod bodies in stomachs, suggesting that beaks persist longer in gizzards and are thus disproportionately represented in seabird diet studies.

The variety of prey found in this study and in the northwestern Pacific (Ogi, this volume), the northeastern Atlantic (Brown *et al.* 1981), and in Monterey Bay during other years (Baltz and Morejohn 1977, Morejohn *et al.* 1978) suggests that Sooty Shearwaters feed on any appropriately sized prey concentrated near the surface; in the North Pacific Ocean, fish predominate.

Table 2
Two-way analysis of variance on monthly means of fat content measured by extraction (total $N = 12$) and fat predicted from equation 2, section 4.2 (see Fig. 4)

Source of variation in predicted fat	df	*SS*	*MS*	*F*	*P*
Among months	5	41.5	8.4	50.9	0.0001
Predicted *vs.* extracted	1	0.01	0.01	0.1	0.8
Error	141	23.3	0.2		
Total	147	65.3			

6.2. Fat and energy gain

Sooty Shearwaters are lean and in moult when they arrive off California in May; they complete their moult between May and August and fatten before departing southward in late summer. During this study, heavy moult in July coincided with a 12% loss of body weight and stored fat (Figs. 3 and 4), suggesting that moult substantially affects energy balance.

The birds fatten rapidly once moult is complete. As in migratory passerines and waterfowl, water content and non-fat body components remain constant while fat increases (Odum *et al.* 1964, Raveling 1979). Minimum fat content (0.03 g/g lean dry weight, or 67 g; see Fig. 4 and equation 3) is similar to the minimum fat content reported for nearly grown, 800 g Herring Gull chicks (*Larus argentatus*) and of migratory passerines (Odum *et al.* 1964, Dunn and Brisbin 1980). This amount probably represents structural tissue that is not extractable with petroleum ether and may not be usable as fuel (Odum *et al.* 1964). Maximum Sooty Shearwater fat levels lie within the range observed by Odum *et al.* (1965) for "very fat fall migrant [passerine] species" (2.0–3.5 g/g lean dry weight).

Several interacting factors could be responsible for pre-migratory fattening. It may occur simply because the energy budget becomes positive after moult or because of a change in some cellular fat setpoint (W. Bennett, pers. comm.). Studies on caged passerines have shown that rapid pre-migratory fattening results from hyperphagia induced by changing day-length acting on the hypothalamus (Odum 1960, Farner *et al.* 1968). Among Shooty Shearwaters, increasing numbers of feeding flocks observed at sea or an increase in the proportion of full stomachs in August–September might signal increased feeding rates, but such changes did not occur during this study. Although hyperphagia may exist, increased prey abundance or availability could also cause fattening. Another possibility is that the available prey could be higher in calories.

The caloric content of Sooty Shearwater prey off California varies (Table 3); therefore the amount of a single prey type that would meet energy needs at various stages in the annual cycle would also vary. Unfortunately, a shearwater's daily energy use is unknown. Energy requirements can, however, be estimated from the following equation for

Figure 3
Progress of moult among Sooty Shearwaters collected in Monterey Bay. Upper plot shows the mean percent of wing and body moult completed per bird for each month; lower plot shows the mean percent of growing wing and tail feathers per bird for each month. Vertical lines are 95% confidence intervals; numbers are sample sizes

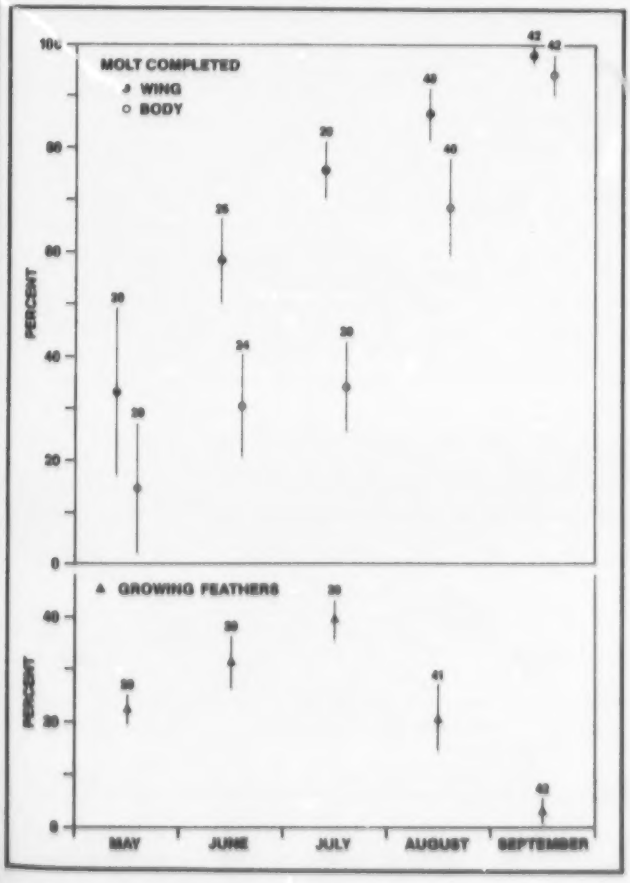
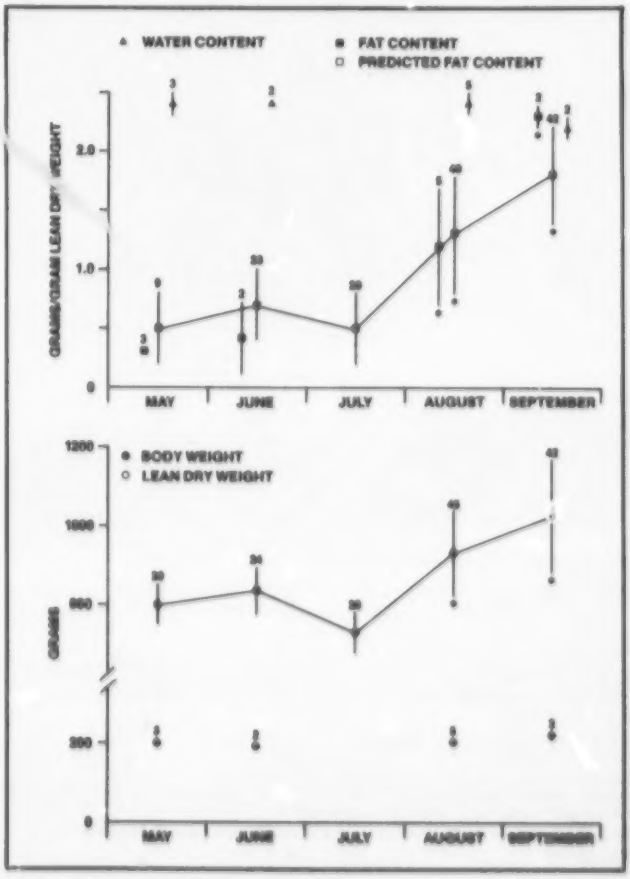


Figure 4
Changes in body weight, lean dry weight, water, and fat content among Sooty Shearwaters from Monterey Bay (means ± SD); numbers are sample sizes. Asterisks indicate mean weights and fat levels that differ significantly from the rest (for further explanation, see text)



the daily energy expenditure (*DEE*) of a free-living non-passerine:

$$\log DEE = \log 317.7 + 0.7052 \log W,$$

where *DEE* is in kcal/day and *W* is body weight in kilograms (J.R. King 1974:39). From May through July, an average Sooty Shearwater weighs about 800 g and would therefore require 271 kcal/day to maintain its body weight (*cf.* Krasnow 1978). With more fat in August and September, however, mean weight exceeds 1000 g. In Monterey Bay fat increases averaged 142 g per bird in August and an additional 115 g in September. Since the caloric value of one gram of stored fat is approximately 9.0 kcal (Odum *et al.* 1965), August and September fat gains corresponded to 1278 kcal and 1035 kcal, respectively. Assuming an 81% assimilation efficiency for fish and 80% for squid and euphausiids (Krasnow 1978), the number of kcal needed per day would be

$$\text{kcal per day} = \frac{\text{kcal of fat increase per month}}{\text{assimilation efficiency}} \times 30 \text{ days/month}$$

Figure 5
Heavy skin and perivisceral fat

Sooty Shearwaters must have consumed at least 324 kcal per day from July to August and 367 kcal per day from August to September to put on the additional fat. The number of "meals," or full stomachs, per day that would meet these caloric requirements would equal

$$\text{kcal required} / (\text{kcal/meal}) \times \text{assimilation efficiency}$$

Changes in diet coincided with these changes in fat. In May–July, the diet consisted of 92% rockfish and 8% market squid, but in August–September when fat was increasing, oily anchovies made up 89% of the diet. Perhaps the late-summer abundance of anchovies in Monterey Bay facilitates pre-migratory fattening in Sooty Shearwaters there. Birds eating an average of 2.7 rockfish meals per day in May–July (Table 3) would be able to store fat in August–September on about the same number of meals per day of anchovies. Reduced anchovy availability might require a shift to lower-calorie prey such as squid or euphausiids. If these species were not available, or if the energetic cost of feeding longer or more often were disproportionately high, fat deposition could decrease substantially. Sooty Shearwaters are believed to feed little or not at all during the long return migration to the southern hemisphere (W.B. King, 1974; Imber, pers. comm.). If true, the amount and efficiency of fat deposition off California could determine migratory success.

7. Acknowledgements

I wish to thank L.D. Krasnow and M.R. McLandress for expert technical advice in the early stages of this project and K.T. Briggs, C. Harrold, W. Landing, D.B. Lewis, and R.L. Pitman for help collecting specimens. T. Burns, M. Pierson, D. Ringo, and J. Schubert provided indispensable field and laboratory assistance. Freeze-drying and extraction equipment was furnished by the University of California at Santa Cruz and Lawrence Livermore Laboratories. J.E. Fitch identified fish otoliths from southern California samples; F.G. Hochberg identified the cephalopod beaks. A.D. Arias and D.L. Garrison engineered many of the statistical and computer analyses. I am grateful to D.G. Ainley, J.P. Croxall, D.L. Garrison, M.J. Imber, L.D. Krasnow, D.C. Potts, R. Ricklefs, and G.A. Sanger for reviewing the manuscript. D.M. Briggs and M.O. Pierson prepared the figures. Without the contributions of these and many other colleagues, this paper could not have been completed.

This work was supported by contracts AA530-CT7-36 and AA551-CT9-33 from the Bureau of Land Management to the University of California, Santa Cruz and by the Center for Coastal Marine Studies, UC Santa Cruz.

Table 5
Caloric value and estimated "meal" size for prey captured by Sooty Shearwaters in Monterey Bay and southern California

Prey	Wet wt, g	Wet wt, kcal/g*	Meal,† g	kcal/ meal	No. of meals per day: May–July 271 kcal	August 324 kcal	September 367 kcal
Engraulis mordax	25*	1.54	100	154	2.2	2.6	2.9
Sebastes spp.	5*	1.35	90	122	2.7	3.3	3.7
Loligo opalescens	20‡	1.23	80	98	3.5	4.2	4.7
Thysanoessa spinifera	0.15‡	0.98	33	32	10.6	12.6	14.2

*Wiens and Scott (1975), Brown *et al.* (1981).
†This study: mean number of prey per full stomach times wet weight.
‡This study.

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Appendix 1
Prey taxa identified from beaks, otoliths, or eye lenses in Sooty Shearwaters collected off California

Location and prey taxa	% occurrence	Number
A. Monterey Bay (*N* = 154)		
Fish*	97.4	4485
Clupea harengus	0.6	2
Engraulis mordax	41.6	266
Ophiodon sp.	0.6	1
Sebastes spp.	22.7	1007
Cephalopods*	94.8	1582
Gonatus spp.	40.3	125
Histioteuthis heteropsis	9.1	21
Loligo opalescens	68.8	942
Onychoteuthis borealijaponicus	29.2	117
Octopus rubescens	19.5	85
Vampyroteuthis infernalis	1.3	2
Polychaetes	4.5	
Plastic pieces	48.7	381
Other†		
B. Southern California (*N* = 37)		
Fish*	94.6	1275
Citharichthys sp.	8.1	13
Engraulis mordax	27.0	7
Merluccius productus	51.4	649
Otophidium scrippsi	2.7	1
Sebastes spp.	62.2	580
Tarletonbeania crenularis	5.4	23
Triphoturus mexicanus	5.4	2
Cephalopods*	78.4	140
Gonatus spp.	18.9	12
Histioteuthis heteropsis	2.7	2
Loligo opalescens	35.1	54
Onychoteuthis borealijaponicus	8.1	13
Onychoteuthis/Gonatus spp.	35.1	46
Octopus rubescens	5.4	2
Polychaetes	2.7	
Plastic pieces	51.4	121
Other†	5.4	

*Includes unidentified material.
†Includes feather lice, algae, sand, pebbles, charcoal.

Further evidence for olfactory foraging by Sooty Shearwaters and Northern Fulmars

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1. Abstract

Our earlier work showed that certain procellariiform species off the central California coast are selectively attracted from downwind to various food-related odours, including cod-liver oil. We here compare the attractiveness of a volatile fraction of cod-liver oil to that of the whole oil, and of homogenates of squid and of krill. All birds in the study area were identified to species, and data are presented here for the Northern Fulmar (*Fulmarus glacialis*) and Sooty Shearwater (*Puffinus griseus*). Comparative data are presented for the Western Gull (*Larus occidentalis*), Common Loon (*Gavia immer*), and Common Murre (*Uria aalge*). The fulmars and shearwaters arrived sooner and more reliably with the cod-liver-oil fraction than with the whole oil, suggesting that volatility was an important factor. Shearwaters also flew upwind to squid and krill. Neither procellariid was sighted when seawater or heptane controls were used alone. Nonprocellariids showed no differential behaviour with respect to stimulus or wind direction. These data, collected with careful controls from October to May throughout a range of weather conditions, strengthen the conclusion that some procellariiform species are attracted by odours related to their natural prey.

2. Résumé

Nos travaux précédents ont montré que certaines espèces de procellariiformes au large de la côte du centre de la Californie étaient attirées de façon sélective sous le vent par différentes odeurs associées à la nourriture, y compris l'huile de foie de morue. Dans le présent article, nous comparons l'attirance d'une fraction volatile de l'huile de foie de morue à celle de l'huile entière et d'homogénats de calmars et d'euphausiacés. Tous les oiseaux dans la zone d'étude ont été identifiés à l'espèce, et les données sont présentées ici pour le Fulmar boréal (*Fulmarus glacialis*) et le Puffin fuligineux (*Puffinus griseus*). Des données comparatives sont fournies pour le Goéland de l'Ouest (*Larus occidentalis*), le Huard à collier (*Gavia immer*) et la Marmette commune (*Uria aalge*). Les fulmars et les puffins étaient attirés plus tôt et de façon plus sûre avec la fraction de l'huile de foie de morue qu'avec l'huile entière, ce qui laisse croire que la volatilité était un facteur important. Les puffins volaient aussi au vent en direction des calmars et des euphausiacés. Nous n'avons vu aucun procellariidé quand nous utilisions, seuls, des témoins faits d'eau de mer ou d'heptane. Les non-procellariidés ne montraient pas de comportement différenciel selon le stimulus ou la direction du vent. Ces données, recueillies avec minutie d'octobre à mai sous tout un éventail de conditions météorologiques, renforcent la conclusion que certaines espèces de procellariiformes sont attirées par des odeurs rappelant leurs proies naturelles.

3. Introduction

In studies of the feeding ecology of seabirds, less attention has been given to how birds find prey than to the types of prey eaten and to where and how they are taken. The dominant guidance is assumed to be visual (e.g. Sealy 1973, Hoffman *et al.* 1981), with possible auditory cues from prey and other birds, but the literature is relatively silent not only on this specific application but also on visual and auditory physiology of seabirds in general.

The specialized interior nasal anatomy and unusually large olfactory mucosae, nerves, and bulbs in many procellariiforms (Bang 1966) suggest olfactory guidance in feeding, a possibility supported by early anecdotal accounts and field notes (reviewed by Wenzel 1980). Recent research has provided direct evidence. Grubb (1972) reported that Leach's and Wilson's storm petrels (*Oceanodroma leucorhoa, Oceanites oceanicus*) and Greater Shearwaters (*Puffinus gravis*) made upwind approaches to a sponge soaked in cod-liver oil more often than they did to one soaked in seawater. The very few Sooty Shearwaters (*P. griseus*) sighted did not approach either sponge. Four other species (*Fratercula arctica, Larus argentatus, Morus bassanus*, and *Sterna paradisaea*) were seen once and showed no systematic reactions to the sponges. In a more extensive study (Hutchison and Wenzel 1980), procellariiforms common off the central California coast were attracted from downwind in daylight by odours of fish oils and vegetable oil but not by mineral oil, seawater, or petroleum oil. By contrast, nonprocellariiforms were not affected and appeared as frequently upwind as downwind. Once attracted from downwind, procellariiforms were more likely to fly close to the source, sometimes repeatedly. Many of their approaches followed a zigzag course, narrowing closer to the odour source, as if following a trail. Close approaches and landings by non-procellariiforms occurred regularly when popcorn or puffed cereal was spread on the water but such visual stimuli had little effect on procellariiform behaviour.

The present study extends information learned from our earlier observations by documenting birds' responses to odours of their own prey and to the volatile portion of cod-liver oil, a readily available material of proven attractiveness but not associated with fish normally eaten by fulmars and shearwaters. Greater potency of the volatile fraction would emphasize the significance of an airborne stimulus.

4. Methods

Tests were conducted with whole cod-liver oil; the volatile fraction of cod-liver oil collected in heptane; homogenized squid (*Loligo opalescens*); homogenized krill (*Euphausia superba*) made from frozen krill obtained from Sea World in San Diego, California; heptane; and seawater as controls. The behavioural responses to each stimulus were analysed for the most plentiful species throughout the testing period, *viz.*, Northern Fulmar (*Fulmarus glacialis*), Sooty Shearwater, Western Gull (*L. occidentalis*), Common Loon (*Gavia immer*), and Common Murre (*Uria aalge*).

All testing was done during daylight in Estero Bay off Morro Bay, California, the same area as we used for our earlier work. Locations varied from 4 to 64 km from shore between longitudes 120 and 122°W and latitudes 35 and 36°N (Fig. 1). Data were collected under a wide range of weather conditions during 50 cruises evenly distributed from October 1980 through May 1981, aboard either of two boats — a 9-m sailboat or a 17-m commercial fishing vessel. Whole cod-liver oil was presented in 49 tests on 40 cruises, cod-liver-oil fraction in 24 tests on 17 cruises, squid homogenate in 20 tests on 19 cruises, and krill homogenate in 11 tests on 10 cruises. For experimental controls, seawater was used in 17 tests on 17 cruises, and heptane in 9 tests on 9 cruises. Tests with whole cod-liver oil, squid homogenate, and seawater were made each month of the study; tests with the other stimuli occurred during the last 4 months.

In the present tests, unlike our earlier ones (Hutchison and Wenzel 1980), we used one method of presenting stimuli, which was a standardized refinement of the final technique developed in the previous study. Odour diffused from a cotton wick on a wire frame that protruded about 3 cm from a 400-mL bottle mounted in a gimbal atop a pole 3.5 cm in diameter and 1 m high. The pole was attached to a float made of an inflated tire inner tube, 110 cm in diameter, with a wooden floor (Fig. 2). One to six hours before testing, whole cod-liver oil, squid homogenate, and krill homogenate were put into bottles. Seawater was bottled at sea shortly before each test, and the highly volatile cod-liver-oil fraction and heptane were transferred from their tightly-sealed containers to bottles immediately before releasing the float. The sample size for each test substance was 150 mL.

To start a test, we uncapped the bottle, inserted a wick, placed the bottle in the gimbal, and put the float overboard when no birds were visible. The boat moved approximately 100 m away in the crosswind direction and a sea anchor was deployed to minimize drift of the vessel. Most tests lasted 90 min. We recorded all species sighted, their locations relative to the wind, the distance of the closest approach to the wick, the direction of departure, and other behaviour patterns of interest. The position, date, time, weather, sea conditions, and bottom characteristics were noted. We stored all data on floppy discs using a Sol micro-computer, for subsequent analysis on an IBM 3033 computer.

At least three observers were present on all trips; any discrepant opinions about species identification or behaviour were settled after each test. We identified birds with

Figure 1
Map of the study area

Figure 2
Float with stimulus bottle and wick attached

the aid of binoculars and took photographs of anything of special interest, including close approaches. Successive tests were separated by 20–90 min depending on the presence of birds, condition of equipment, and special problems. Whenever possible, seawater and heptane were presented at the same locations as the experimental odours. Some cruises were interrupted by poor weather, mechanical problems, or minor accidents so test schedules had to be flexible.

Squibb or Nature's Best whole cod-liver oil was used for the early tests in this series; for the later majority of experiments, oil was obtained in 3–4 gallon amounts from J.A. Sanborn Co., Boston, Massachusetts. The volatile fraction was prepared from the whole oil by vacuum extraction and collected in reagent-grade heptane as solvent. Each 150 mL of solvent included approximately 0.5% cod-liver-oil volatiles. Squid homogenate was made from fresh or freshly thawed animals in a heavy-duty Waring blender. The krill was homogenized in a different blender.

5. Results

In close agreement with our earlier results (Hutchison and Wenzel 1980), approaches of Northern Fulmars and Sooty Shearwaters were almost entirely (77–100%) downwind of the wick after release of all four experimental stimuli (Table 1, Figs. 3–6), and were sighted only once or not at all during control tests with heptane and seawater (Table 1, Figs. 7 and 8). Chi-square tests of the distributions of sightings by wind direction showed that the shearwaters were sighted significantly more often downwind than either upwind or crosswind in the tests with whole cod-liver oil and the fraction ($p<0.001$). With squid homogenate, 29 of 30 shearwater sightings were downwind and with krill homogenate, 21 of 26 sightings were so; crosswind and upwind frequencies were thus too low for a chi-square test.

Table 1
Total number of each species sighted with each stimulus, the percent downwind (% *DW*), and the mean number sighted per test (*M*/test)

Stimulus	Northern Fulmar	Sooty Shearwater	Western Gull	Common Loon	Common Murre
Cod-liver oil					
Whole					
Sightings	23	60	124	48	223
% *DW*	83	77	32	25	37
M/test	0.5	1.2	2.5	1.0	4.6
Fraction					
Sightings	7	43	60	26	29
% *DW*	100	84	25	92	10
M/test	0.3	2.0	2.9	1.2	1.4
Squid					
Sightings	4	30	41	16	99
% *DW*	100	97	51	25	63
M/test	0.2	1.5	2.0	0.8	5.0
Krill					
Sightings	1	26	25	20	9
% *DW*	100	81	40	85	0
M/test	—	2.2	2.1	1.7	0.8
Heptane					
Sightings	0	0	20	2	6
% *DW*	—	—	26	50	67
M/test	0	0	2.2	0.2	0.7
Seawater					
Sightings	1	1	42	20	67
% *DM*	0	0	60	90	34
M/test	—	—	2.5	1.2	3.9

Fulmar counts were high enough to permit statistical analysis only for the tests with whole cod-liver oil when their downwind approaches were significantly more frequent than either of the other directions ($p<0.05$). In seawater tests, one fulmar and one shearwater were sighted, each crosswind, and no sightings of either species occurred in tests with heptane.

No consistent pattern of direction related to our experimental or control stimuli was seen in the three species of nonprocellariiforms (Table 1, Figs. 3–8). During the tests with cod-liver-oil fraction, most Common Loons were sighted downwind, which corresponded to their migratory path

Figure 3
Direction of sighting and closest approach for each species during all tests with whole cod-liver oil. Numbers of birds are depicted as percentages for comparability; absolute totals sighted are shown below each chart. The float is at the centre; the inner circle is 10 m away from it, the outer circle 50 m. To illustrate interpretation, of the 23 Northern Fulmars sighted during 49 tests, 30% were downwind and approached within 11–49 m of the float, 52% were downwind and approached within 10 m, and 9% were crosswind and approached within 10 m

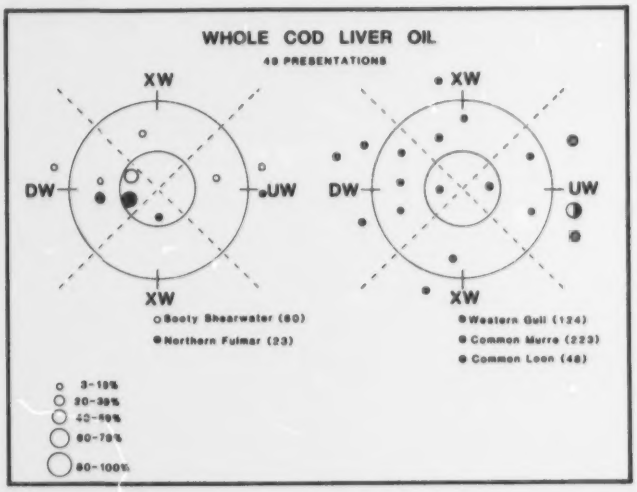
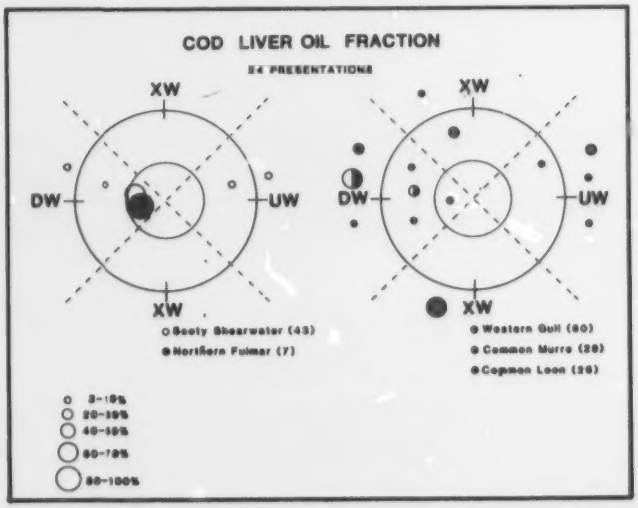


Figure 4
Direction of sighting and closest approach for each species during all tests with cod-liver-oil fraction in heptane. See legend of Fig. 3



through our study area. So few loons were seen flying in other directions that no chi-square could be calculated for directional differences. Conversely, during tests with whole cod-liver oil, Common Loons were sighted significantly most frequently upwind of the stimulus ($p<0.01$). The same reversal occurred for Western Gulls (whole cod-liver oil, upwind most frequent, $p<0.001$; cod-liver-oil fraction, downwind most frequent, $p<0.05$). Common Murres were either evenly distributed across directions or so densely located in only one that statistical analysis was meaningless.

In further verification of the attractiveness of our test materials, the fulmars and shearwaters flew close to the wick when food-related stimuli were being released (Figs. 3–6). With whole cod-liver oil, the fulmar's approaches from downwind to within 10 m were significantly more frequent than all other combinations of distance and direction (chi-square test, $p<0.05$). Frequencies for fulmars in tests with other odours were too low for analysis, although all seven fulmar approaches to the cod-liver-oil fraction were from downwind and within 10 m. Their four approaches to squid were from downwind but only one was within 10 m. The one fulmar sighted during tests with krill was downwind and approached closer than 50 m. The shearwaters' close approaches from downwind were significantly greater than all other combinations with each of the four experimental stimuli (whole cod-liver oil, $p<0.001$; cod-liver-oil fraction, $p<0.001$; squid homogenate, $p<0.01$; krill homogenate, $p<0.05$).

By contrast, nonprocellariiforms seldom flew closer than 50 m to the wick. Loons most commonly passed at 50 m or more from both the whole oil and the fraction ($p<0.01$ each). With squid homogenate, all of their flights were at these distances; with krill homogenate the frequencies were too scattered for analysis. Western Gulls also passed at the outer distance. No gull made a close approach from any direction with krill homogenate and only one did so, crosswind, with cod-liver-oil fraction. With the other two food-related stimuli, also, 50 m or more was their most frequent distance (whole cod-liver oil, $p<0.001$; squid homogenate, $p<0.01$). Common Murres made only five close approaches out of 359, none from downwind, and these five involved three different stimuli.

The procellariids' close approaches often followed the zigzag path described earlier (Hutchison and Wenzel 1980). Rather than flying straight toward the float, they crisscrossed the area downwind of it with progressively shorter traverses, as if following an odour trail. Upon

Table 2
Average ambient wind velocity (km/h) and approach latency (min) to whole cod-liver oil and cod-liver-oil fraction in heptane by Northern Fulmars and Sooty Shearwaters, and the correlation of wind velocity and the birds' approach latency (VL), their mean number of circuits around the float, and the correlation of their circling frequency with wind velocity (VC)

	Velocity (km/h)	Latency (min)		Circuits	
	Mean ± SD	Mean ± SD	r_{VL}	Mean ± SD	r_{VC}
Whole oil					
Fulmars	13.2 ± 8.7	21.5 ± 2.0	−0.04	1.4 ± 1.3	0.16
Shearwaters	14.2 ± 7.7	20.4 ± 2.3	−0.03	1.3 ± 1.1	0.28
Oil fraction					
Fulmars	18.5 ± 8.4	7.3 ± 1.4	−0.24	3.6 ± 1.3	−0.55
Shearwaters	15.8 ± 10.9	7.4 ± 2.2	−0.21	1.8 ± 1.5	0.25

Figure 5
Direction of sighting and closest approach for each species during all tests with squid homogenate. See legend of Fig. 3

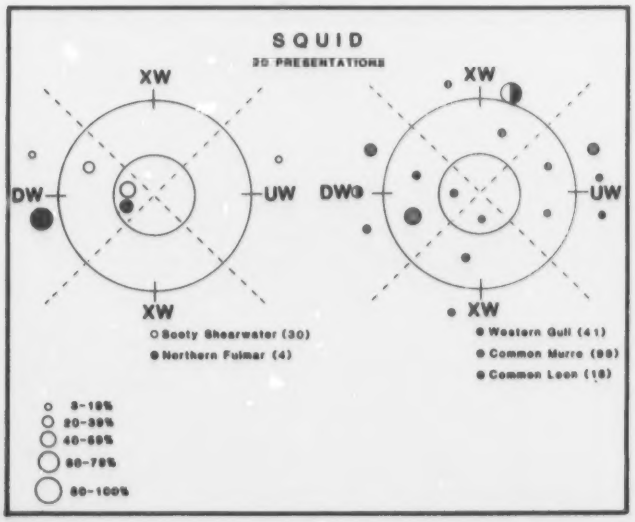
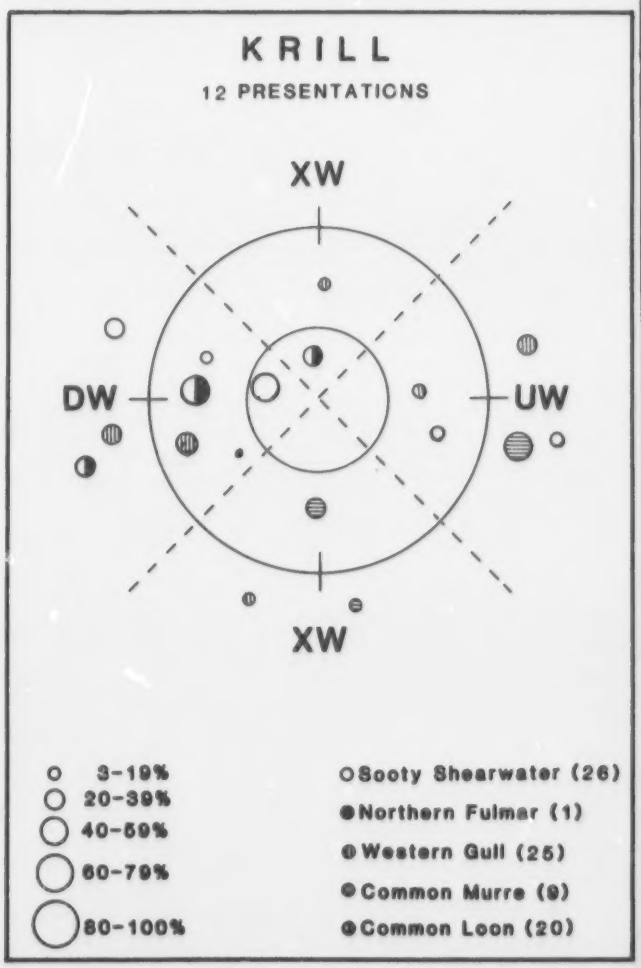


Figure 6
Direction of sighting and closest approach for each species during all tests with krill homogenate. See legend of Fig. 3



reaching the float, birds usually circled it from one to five times before flying away. They never landed on the float or flew directly toward the observation boat. Occasionally, a bird would land on the water, 10–20 m downwind of the float and stay for 5–10 min.

The cod-liver-oil fraction was a more potent attractant than the whole oil. Fulmars or shearwaters approached on 91% of the tests with the fraction compared to 47% of tests with the whole oil, and approaches within 10 m were more common (Figs. 3 and 4). Table 2 shows the mean latencies of downwind sightings of fulmars and shearwaters that approached within 50 m during tests with both stimuli. Frequency distributions of latencies were normalized by logarithmic conversion of each score and differences between stimuli were tested by the t-test. For each species, the latency was significantly shorter with the fraction than with whole oil ($p<0.001$). Mean wind velocities during these tests were comparable (Table 2) and could not account for the differences. We have no direct measure of the diffusion rates of the two preparations but greater volatility insures faster vaporization, resulting in earlier arrival of molecules at a given distance downwind. Neither latency nor circling behaviour was correlated with wind velocity for either species with either preparation (Table 2). The mean number of circuits flown around the wick by fulmars was significantly ($p<0.01$) greater with the cod-liver-oil fraction (Table 2). Every fulmar sighted during tests with the fraction not only approached closely but also circled at least twice and every shearwater circled at least once. With the whole oil, shearwaters failed to circle on 28% of their close approaches and fulmars made no circles on 38% of such approaches.

The mean visibility was 25 km for all cruises, with the great majority at 16 or better. The lowest values were 5–10 km, accompanied by light to medium fog. These conditions occurred when fulmars were in the study area, during tests in January, February, and March, and they were most frequently attracted to the food-related odours on such days. Shearwaters, on the other hand, showed an opposite effect, being most likely to approach on days with high visibility ($p<0.01$).

Fulmars made almost no approaches to squid or krill homogenate, although tests with krill did not start until shortly before they usually leave our study area. They approached the cod-liver-oil stimuli in the same period, however. Shearwaters were strongly attracted to both. They

Figure 7
Direction of sighting and closest approach for each species during all tests with heptane. See legend of Fig. 3

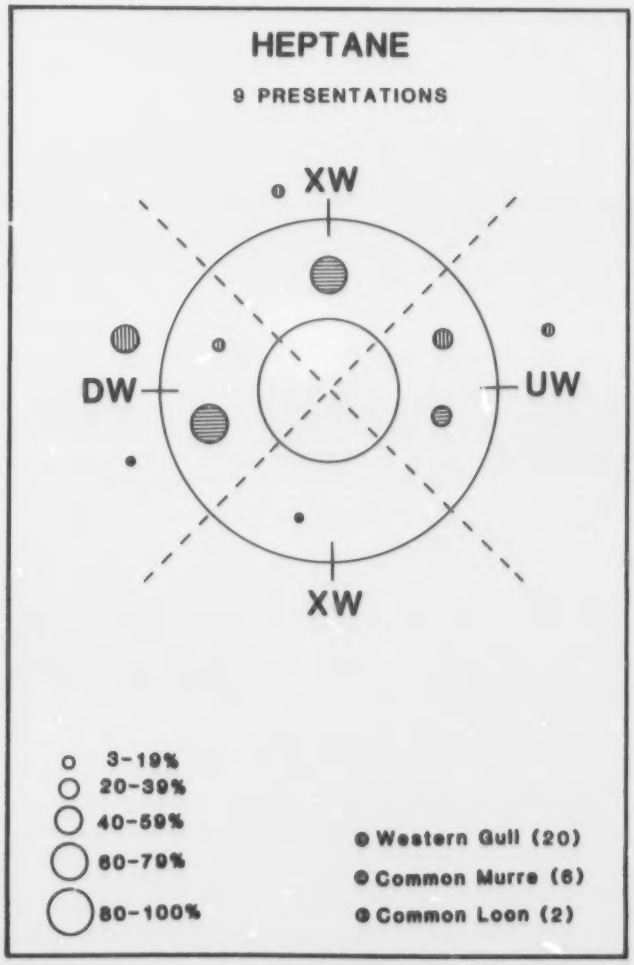
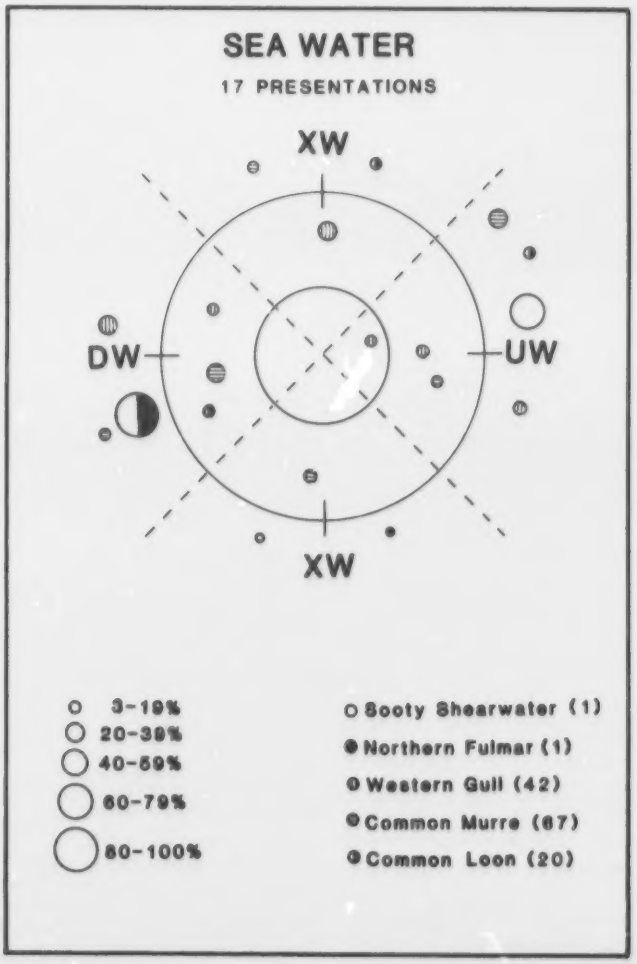


Figure 8
Direction of sighting and closest approach for each species during all tests with seawater. See legend of Fig. 3



approached closely on 75 and 73%, respectively, of the tests with squid and krill. In these tests, also, they appeared predominantly on days with high visibility. Their mean approach latencies were 16.6 and 21.5 min, comparable to their latencies with whole cod-liver oil (Table 2). They averaged 2.2 and 2.8 circuits on each close approach, significantly ($p<0.01$) more than with whole cod-liver oil (Table 2).

The prevailing wind in Estero Bay is from the northwest, and throughout the test period winds were in the quadrant between west and north 70–80% of the time. The fact that the procellariids' upwind approaches to our stimuli were oriented generally northwest through the test period means that they were not simply migrating.

6. Discussion

These data confirm and extend our previous work (Hutchison and Wenzel 1980) showing reliance on olfaction in foraging by Northern Fulmars and Sooty Shearwaters. The faster and closer approaches to the volatile fraction of cod-liver oil compared to the whole oil support the conclusion that airborne stimuli are used for guidance by these species. Furthermore, the attractiveness of odours of squid and krill for Sooty Shearwaters, two dietary components for these birds (Chu, this volume), strongly suggests that olfactory guidance is normally used to find prey. Such conclusions imply that foraging would be better in areas with enough wind to disperse odorous molecules over a significant distance. Our lack of correlation between wind velocity and both approach latency and circling, however, shows that high winds do not necessarily increase investigative behaviour. Odour quality is probably as important as the intensity.

Other sensory systems may also be important to fulmars and shearwaters in foraging. In their extensive pelagic habitat, with its infinite variations of weather and visibility, however, it would be highly advantageous to have well-developed detection systems for smell as well as sight. Olfaction may be especially helpful when visibility is low. Several times fulmars approached our experimental stimuli from downwind during fog and limited visibility, and many procellariids are known to feed at night (Gould 1967, Wenzel 1980). The use of olfaction is not restricted to poor visibility, however, as shown by our present results when visibility was generally much better than previously (Hutchison and Wenzel 1980). The greater tendency of fulmars than shearwaters to approach during lower visibility may be due partly to greater frequency of such conditions in the months when Northern Fulmars are plentiful off central California. This explanation does not account for their scarce appearances on completely clear days in the same period, but the impression persists that they were more responsive to odours during limited visibility.

Our high rate of success in attracting Sooty Shearwaters to odours of squid and krill suggests a resemblance to natural foraging. We do not know what odours are associated with these prey in nature. Under our conditions, these crude preparations were as effective as whole cod-liver oil as measured by latency of approach, and as effective as the volatile fraction of cod-liver oil as measured by the number of circles flown around the wick. Sooty Shearwaters have been identified as a principal catalyst of seabird feeding flocks in Alaska (Hoffman *et al.* 1981). It may be that they are aided by smell in locating plentiful supplies of fish or euphausiids and the sight of their feeding behaviour then attracts other birds. Black-legged Kittiwakes (*Rissa tridactyla*) are also said to start feeding flocks (Sealy 1973, Hoffman *et al.* 1981). Their olfactory anatomy has never been examined; possibly they, too, have large amounts of primary olfactory tissue. Procellariids may not be alone among seabirds in olfactory ability.

7. Acknowledgements

This work was supported by grant no. 2224-80 from the National Geographic Society and grant no. BNS-8013049 from the National Science Foundation. Chemical consultation was given by Orville L. Chapman, Department of Chemistry, University of California at Los Angeles, where the cod-liver-oil fractions were prepared by Steven Pitzenberger. Krill was provided by Frank Todd and Scott Drieschman at Sea World, San Diego, Calif. Help with various tasks on the boats was given at different times by Bart Alford, Forrest Doud, Ron Field, Bruce Marshall, Ron Randrup, and Don Schroeder. Martin Echols was responsible for computer programming, assisted by Ron Field. Diagrams were prepared by V. Susan Fox.

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Feeding ecology of the Sooty Shearwater in the western subarctic North Pacific Ocean[1]

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1. Abstract

Stomach contents from 173 Sooty Shearwaters (*Puffinus griseus*) taken in deep, oceanic waters of the western subarctic North Pacific from spring to autumn, 1975–80 (except for 1976) were examined. By weight, fish was the most important food item (83.1%), particularly Pacific saury (*Cololabis saira*) which comprised 69.7% of stomach contents. Squid, the next most important prey, may have been underestimated due to a rapid rate of digestion. Squid increased and the saury decreased in importance with increasing latitude.

The prevalence of saury in the diet, by weight, shifted northwards in oceanographic areas with time: in June 78.1% in the Subtropic Region and 88.1% in the Transition Domain; in July 26.6% in the Transition Domain; in August 84.4% in the Transition Domain, 62.9% in the Subarctic Current, and 30.1% in the Alaskan Stream; in September and October 99.2% in the Subtropic Region, 89.0% in the Transition Domain, and 88.1% in the Subarctic Current. The prevalence of squid in the diet did not change with time. Sea surface temperatures (SST) ranging from 9 to 13°C at localities where numerous Sooty Shearwaters were often observed feeding were also favoured by shoals of saury; both the shearwater and saury moved northwards as SSTs warmed. The movements of Sooty Shearwaters in pelagic subarctic waters of the North Pacific may be related directly to change in the physical environment and to the availability of suitable prey.

2. Résumé

Nous avons examiné le contenu stomacal de 173 Puffins fuligineux (*Puffinus griseus*) recueillis dans les eaux pélagiques de l'ouest de l'océan Pacifique Nord subarctique, du printemps à l'automne, de 1975 à 1980 (sauf 1976). En poids, les poissons étaient l'aliment prédominant (83,1 %). Nous reconnaissions surtout le balaou japonais (*Cololabis saira*) qui constituait 69,7 % du contenu stomacal. Le calmar, la deuxième proie en importance, peut avoir été sous-estimé à cause de sa rapidité de digestion. Plus nous allions au nord, plus l'importance du calmar augmentait et plus celle du balaou diminuait.

Avec le temps, la prédominance, en poids, du balaou dans le régime changeait à mesure que nous montions vers le nord dans les zones océanographiques : en juin, 78,1 % dans la région subtropicale et 88,1 % dans le domaine de transition; en juillet, 26,6 % dans le domaine de transition; en août, 84,4 % dans le domaine de transition, 62,9 % dans le courant subarctique et 30,1 % dans le courant de l'Alaska; en septembre et octobre, 99,2 % dans la région subtropicale, 89,0 % dans le domaine de transition et 88,1 % dans le courant subarctique. La prédominance du calmar dans le régime ne changeait pas dans le temps. Les températures de la surface de la mer, se situant entre 9 et 13°C à des endroits où nous observions souvent de nombreux Puffins fuligineux en train de se nourrir, étaient aussi préférées par les bancs de balaous. Les puffins et les balaous se déplaçaient vers le nord à mesure que la surface de la mer se réchauffait. Les déplacements des Puffins fuligineux dans les eaux subarctiques pélagiques du Pacifique Nord peuvent être directement reliés aux changements dans le milieu physique et à la disponibilité des proies appropriées.

3. Introduction

The Sooty Shearwater (*Puffinus griseus*) migrates to the northern hemisphere after breeding in the southern hemisphere (Loomis 1921, Phillips 1963, Shuntov 1972), and in the subarctic regions of the North Pacific Ocean during summer it becomes one of the most important components of the marine avifauna. The species' feeding habits while in the northern hemisphere have been studied fragmentarily, and largely in neritic habitats (Wiens and Scott 1975; Baltz and Morejohn 1977; Morejohn *et al.* 1978; Sanger and Baird 1977*a*, 1977*b*; Sanger *et al.* 1978; Brown *et al.* 1981).

In the present study the prey of Sooty Shearwaters was determined for pelagic waters of the subarctic western North Pacific Ocean from June to October. The occurrence of this bird was then viewed in relation to oceanographic conditions and the distribution and migration of prey.

4. Materials and methods

Stomach contents from 173 Sooty Shearwaters that were incidentally entangled in gill nets set for salmon (*Onchorhynchus* spp.) tuna (Family Scomleridae), and squid were used in this study. Stomach samples were collected in 1975, and 1977–80, from the following research vessels: TS *Oshoro Maru* (Os), TS *Hokusei Maru* (Ho), RV *Habomai Maru No. 21* (Hb), RV *Shinyo Maru* (Sh), TS *Hokuho Maru* (Hk), RV *Hoyo Maru No. 67* (Hy), and RV *Hatsue Maru No. 62* (Ht).

[1]Contribution No. 151 from the Research Institute of North Pacific Fisheries, Faculty of Fisheries, Hokkaido University.

To determine the overall seasonal composition of the diet, sampling stations were grouped into four periods (Fig. 1, Table 1). The number of birds sampled in respective periods were as follows: 51 from 13 stations in June, 50 from 8 stations in July, 35 from 11 stations in August, and 37 from 14 stations in September and October. One bird was also caught in April.

Stomach contents in the proventriculus and gizzard of each shearwater were identified and grouped into the following categories: fish, squid, euphausiids, amphipods, shrimp, pelagic barnacles, jellyfish, unidentified digested matter, and other materials. The latter were further classified into fish otoliths, cephalopod beaks, pebbles, vegetable matter (including seaweed, grass seed, and small pieces of wood), and plastic particles.

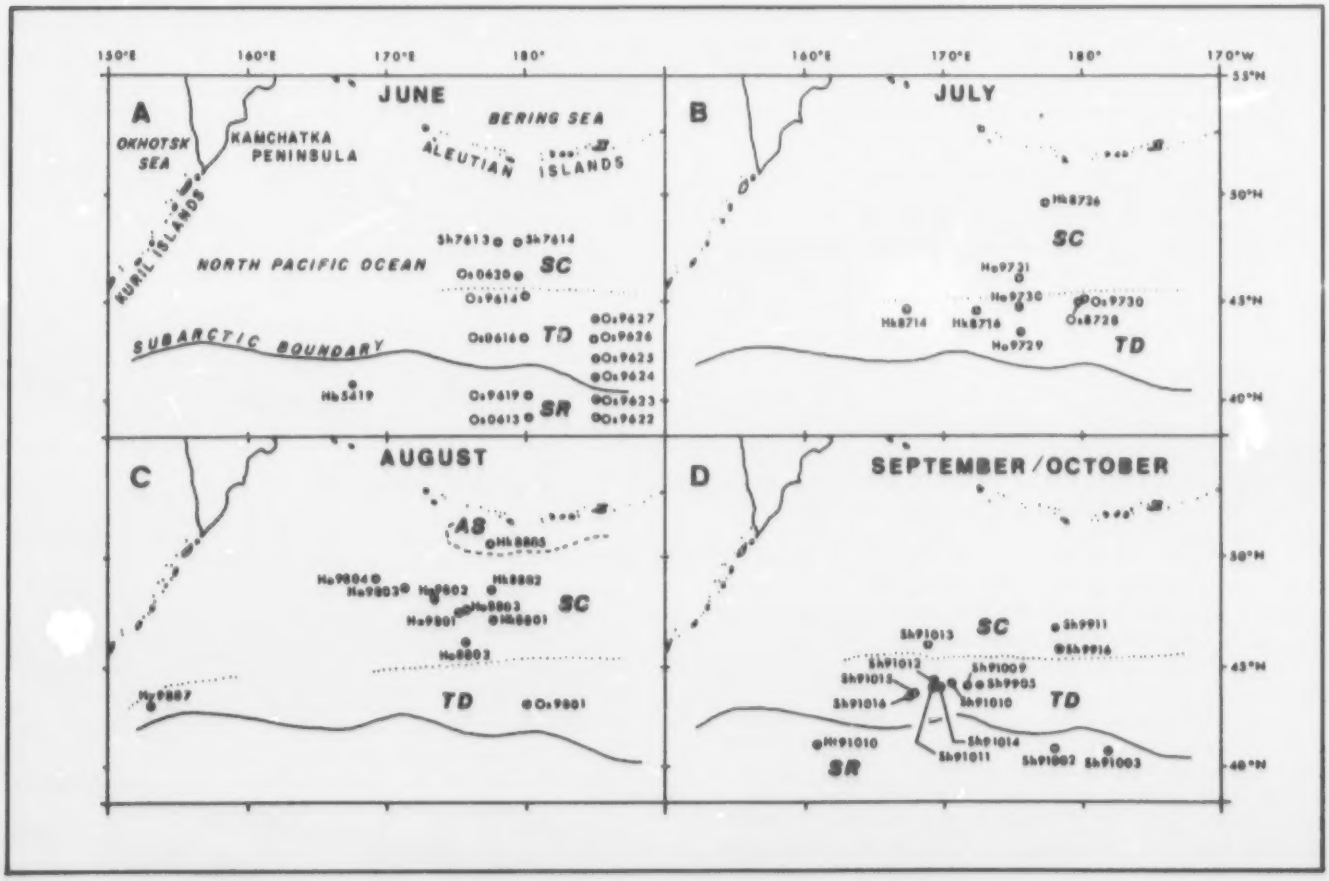
All whole items were weighed wet to the nearest 0.001 g. When possible, items were identified to species. Stomach contents were preserved in neutral formaldehyde solution for up to 6 months, so some otoliths disappeared and others became corroded beyond identification. Eight intact otoliths from three stomachs were identified to family level.

Sampling stations were grouped according to four oceanographic areas (Fig. 1) based on the literature (Dodimead *et al.* 1963; Favorite 1967, Hokkaido Univ. 1976, 1978–82; Kikuchi and Tsujita 1977; Favorite *et al.* 1976; and Ogi 1980) and longitudinal sections of temperature profiles, as follows: along longitude (long.) 167°30′E from latitude (lat.) 39°50′N to 52°30′N during 18–30 April 1975 by RV *Habomai Maru No. 21* (Hokkaido Univ. 1976); along long. 180° from lat. 39°N to 46°N during 12–20 June 1979 and along long. 175°W from lat. 39°N to 45°N during 21–28 June 1979 by TS *Oshoro Maru* (Hokkaido Univ. 1980); along long. 175°30′E from lat. 39°54′N to 47°32′N during 26–31 July 1979 (Hokkaido Univ. 1980) and *ca.* long. 170°E from lat. 35°N to 47°41′N during 28 July – 5 August 1977 by TS *Hokusei Maru* (Hokkaido Univ. 1978). Gill nets were set for fish along all these lines, and all Sooty Shearwaters caught incidentally in these nets were used.

The distribution of Sooty Shearwaters was determined from two sources: the data on gill-netted seabirds by various research vessels from 1969 to 1981 (Ogi, unpubl. data) and seabird sighting data during six cruises from April to November 1979–81 (Ogi, unpubl. data).

Data on the distribution of the Pacific saury (*Cololabis saira*) came from gill nets set by the TS *Oshoro Maru* and TS *Hokusei Maru* (Hokkaido Univ. 1980, 1981 and 1982) and TS *Hatsue Maru No. 62* (Mishima *et al.* 1981). Each of the above vessels used a non-selective net composed of mesh sizes ranging from 25 or 37, to 204 or 233 mm (stretched

Figure 1
Sampling stations for Sooty Shearwaters in the North Pacific in 1975, and 1977–80. (*A*) Black dot denotes April sampling station. (*D*) Black dots denote September sampling stations. AS is Alaskan Stream, SC is Subarctic Current, TD is Transition Domain, SR is Subtropic Region



measurement). In addition to these mesh sizes, additional nets were added that were particularly effective for Pacific saury, albacore (*Thunnus alalunga*), and Pacific salmon. Nets with mesh ranging from 25 to 48 mm were most effective for catching saury. I also used the unpublished sighting records of saury shoals at sea compiled from the logs of various research vessels. The occurrence of saury in bird stomachs was also used to confirm the fish distribution.

Only one bird was caught in April (at station Ib5419 in 1975: Fig. 1A) and squid ranked first in its stomach (64.0% by weight). Also, the sample in September was so small (one bird at each of three stations; Sh9905, Sh9911, and Sh9916: Fig. 1D) those stomach contents data were combined with those from October in the following analysis.

5. Results

5.1. Diet composition by weight percentage

Overall, fish was the most important food item in stomachs by weight (83.1%), followed by squid (7.3%), unidentified digested matter (5.4%), and pelagic barnacles (2.9%) (Table 1). Other items were of minor importance.

Through the months studied, fish was the dominant food item in almost all areas (Table 1). In the Subarctic Current in June and Alaskan Stream in August, however, squid was the top ranking item, respectively comprising 88.9 and 39.8% of the diet, followed by unidentified digested matter (8.2%) in the former and fish (30.1%) in the latter. Squid were not found in bird stomachs in the Subtropic Region. Euphausiids and amphipods occurred only in the Subarctic Current during June and August, whereas pelagic barnacles and jellyfish were found in the Transition Domain and/or Subtropic Region from June to September–October.

5.2. Stomach content weight per bird

Stomach content weights of Sooty Shearwaters (Table 2) were slightly higher than for other species of seabirds, taken in the same areas, such as Short-tailed Shearwaters (*Puffinus tenuirostris*: Ogi *et al.* 1980) and Thick-billed Murres (*Uria lomvia*: Ogi 1980). The maximum stomach content weight was 106.5 g or about 12.3% of the body weight.

5.3. Prey species of the Sooty Shearwater

The prey species and their weights are summarized in Table 3. In all, Pacific sauries were found at 16 out of 47 stations, and in 41 of 173 bird stomachs. During July, this fish was eaten only by shearwaters caught in the Transition Domain, but this may have been an artifact of sampling because six of eight (75%) stations during this month occurred there. The maximum number of fish per bird was two in most cases. Fresh sauries occurred in two stomachs in the Transition Domain during June and one in the Subtropic Region during September–October. The fork lengths of these fish were 160, 175, 190, 209, and 262 mm; the first four of these individuals were immature ("small-sized type" of Odate [1977]) and the last one was an adult ("medium-sized type"). Sauries penetrate into the subarctic North Pacific beyond the Subarctic Boundary during early summer (Odate 1977, Fukushima 1979), and stay in the Subarctic for about 3 or 4 months. Its northward migration into the Subarctic lasts about 3 months. By late August the fish ranges across the entire northwestern North Pacific. Some Pacific sauries reach lat. 55°N in the Okhotsk Sea (Ogi, unpubl. data) and lat. 60°N along the southeastern

Table 2
Weights of Sooty Shearwater stomach contents and their maximum proportion of body weight, by month

Month	*N*	Range, g	Mean, g	*BW*, g*	Percent†
Jun.	51	0.10– 85.01	12.55	814	10.4
Jul.	50	0.06–106.45	5.27	863	12.3
Aug.	35	0.02– 35.07	3.57	844	4.2
Sep.–Oct.	37	0.07– 75.09	11.89	975	7.7

*Body weight of the bird that has the maximum stomach content weight (*BW* does not include the stomach content weight).
†(Maximum stomach content weight/*BW*) × 100 = %.

Table 1
Overall composition of Sooty Shearwater diet by month and sea area

Month	Sea area*	Number of		Weight percentages†							
		Station	Stomachs	F	Sq	E	A	Sh	Ba	Je	dm
Jun.	SC	3	8	0.06	88.9	1.7	1.1	—	—	—	8.2
	TD	6	30	88.3	1.6	—	—	—	6.4	0.7	3.1
	SR	4	13	78.1	—	—	—	—	10.9	8.8	2.1
	Total	13	51	79.9	8.1	0.1	0.09	0	6.6	1.9	3.3
Jul.	SC	2	8	82.5	17.4	—	—	—	—	—	0.09
	TD	6	42	74.9	0.04	—	—	0.6	—	0.7	23.8
	Total	8	50	79.4	10.3	0	0	0.2	0	0.3	9.7
Aug.	AS	1	1	30.1	39.8	—	—	—	—	—	30.0
	SC	8	28	73.4	1.5	7.4	0.2	—	—	—	17.4
	TD	2	6	85.6	—	—	—	—	—	13.6	0.8
	Total	11	35	64.6	11.9	3.3	0.09	0	0	3.7	16.5
Sep.–Oct.	SC	3	4	96.7	—	—	—	—	—	—	3.3
	TD	8	24	89.5	6.1	—	—	—	0.4	—	4.0
	SR	3	9	99.6	—	—	—	—	—	—	0.4
	Total	14	37	95.1	2.4	0	0	0	0.2	0	2.3
Grand total		46	173	83.1	7.3	0.3	0.04	0.04	2.9	1.0	5.4

*AS is Alaskan Stream, SC is Subarctic Current, TD is Transition Domain, SR is Subtropic Region.
†F: fish; Sq: squid; E: euphausiids; A: amphipods; Sh: shrimp; Ba: barnacles; Je: jellyfish; dm: digested matter.

Kamchatka Peninsula in the western Bering Sea (Parin 1968). In early autumn the fish turns southward for its contranatant migration; it spawns and winters in the Subtropic Region (Odate 1977, Fukushima 1979).

A chub mackerel was found in one bird stomach in July in the Transition Domain. Like the saury, this fish also penetrates into the subarctic North Pacific and reaches about lat. 49°N in the Subarctic Current during July (Murakami 1969). In this study this fish species was of minor importance to shearwaters.

A threespine stickleback occurred in one bird stomach in the Subarctic Current in July. In the Subarctic Current and Transition Domain, this species occurred in stomach contents of Short-tailed Shearwaters (*Puffinus tenuirostris*) (Ogi *et al.* 1980), Thick-billed Murres (*Uria lomvia*) (Ogi 1980), Tufted Puffins (*Fratercula cirrhata*), and Horned Puffins (*Fratercula corniculata*) (Ogi, unpubl. data). Several times at night I saw thousands of threespine sticklebacks around the drifting ship in the Transition Domain and Subarctic Current. It would thus seem that Sooty Shearwaters would have the opportunity to feed on this fish during the daytime hours.

In the Subtropic Region, myctophid (lanternfish) otoliths were found from two birds in June and from one bird in October.

In the Subarctic Current in June, a shearwater had eaten four squid whose dorsal mantle lengths ranged from 64 to 84 mm. This was the only squid identified to species in this study.

Barnacles occurred in a total of 13 birds taken at six stations in the Transition Domain and Subtropic Region. On several occasions, I saw a number of shearwaters crowded around a floating log, the surface of which was densely covered with pelagic barnacles. When the ship approached closer, several grazed patches were evident on each log. In this way Sooty Shearwaters were able to feed on these sessile organisms.

Table 3
Prey species of the Sooty Shearwater

Month	Sea area*	Station	*N*†	*n*‡	(No. of prey) prey weight (g) of individual bird (FL or DML)§
a. Pacific saury					
Jun.	TD	Os9626	7	1	(2)45.0(FL: 209 mm) and 39.0(FL: 190 mm)
		Os9625	9	2	10.6, (1)30.7
		Os9624	9	7	46.6, 9.6, 32.2, (2)41.4, (2)45.8 (FL: 175 mm) and 35.2(FL: 160 mm), 36.8, 59.9
	SR	Os0613	3	1	0.6
		Os9619	5	2	(2)40.2, (1)33.4
		Os9623	4	2	2.1, 0.9
Jul.	TD	Ho9729	4	2	(1)26.5, 2.0
Aug.	AS	Hk8805	1	1	10.6
	SC	Ho9803	3	2	8.9, 2.4
		Ho9802	12	2	18.6, 5.3
	TD	Os9801	2	2	6.0, 2.2
		Hy9807	4	2	5.9, 14.4
Sep.–Oct.	SC	Sh9916	1	1	68.2
	TD	Sh91011	2	1	0.6
		Sh91010	11	7	5.0, (2)47.1, 11.1, (2)31.0, 33.8, 12.2, 13.6
	SR	Sh91003	7	6	9.9, 15.0, 13.1, (1)75.1(FL: 262 mm), 36.5, (2)38.6
b. Chub mackerel (*Scomber japonicus*)					
Jul.	TD	Os9730	4	1	(1)43.8(FL: 190 mm)
c. Threespine stickleback (*Gasterosteus aculeatus*)					
Jul.	SC	Hk8726	4	1	(9)15.1
d. Rockfish (*Sebastes* sp.)					
Jul.	SC	Hk8726	4	1	91.3
e. Unidentified fish larva					
Jun.	SC	Sh7614	4	1	(1)0.03
f. Berryteuthis anonychus					
Jun.	SC	Os0620	2	1	(4)44.2(DML: 66, 64, 80, 84 mm)
g. Barnacles (Cirripedia sp.)					
Jun.	TD	Os9626	7	1	7.0
		Os9625	9	5	1.1, 2.0, 1.2, 13.3, 4.4
		Os9624	9	1	2.1
	SR	Os9623	4	4	0.8, 0.2, 4.9, 4.6
		Os9622	1	1	0.4
Sep.–Oct.	TD	Sh91016	3	1	0.7
H. Vellela lata					
Jun.	TD	Os9627	3	2	0.4, 0.1
		Os9626	7	1	2.0
		Os9624	9	2	0.2, 0.7
	SR	Os9619	5	2	4.4, 4.3
Jul.	TD	Os9730	4	1	0.7
Aug.	TD	Os9801	2	1	4.6

*AS is Alaskan Stream, SC is Subarctic Current, TD is Transition Domain, SR is Subtropic Region.
†Number of stomach samples.
‡Number of stomachs in which each prey species occurred.
§FL: fork length (mm) in fish; DML: dorsal mantle length (mm) in squid.

5.4. Seasonal and oceanographic changes in diet

To study the incidence of saury in shearwater stomachs in more detail, I determined the frequency of occurrence (Table 4) and percentage by weight (Table 5) of the Pacific saury in the shearwater diet for each area and month. They appeared in stomachs from the Transition Domain (33.3%) and Subtropic Region (38.5%) during June; only in the Transition Domain (4.8%) during July; and in the Alaskan Stream (one bird), Subarctic Current (14.3%) and Transition Domain (66.7%) during August. Thus by early August saury had occurred in shearwater stomachs across the latitudinal extent of stations sampled in the subarctic North Pacific. From August onward, the occurrence of sauries in bird stomachs continued to be high: in the Subarctic Current, 25%; Transition Domain, 33.3%; and Subtropic Region, 66.7%. In all, the species was found in a minimum of 41 (23.7%) of 173 stomachs.

Based on weight, the importance of saury to shearwaters is even more obvious (Table 5). During June the saury comprised 88.1% of stomach contents weight in the Transition Domain and 78.2% in the Subtropic Region; 26.6% in the Transition Domain during July; 30.1% in the Alaskan Stream (one bird), 62.9% in the Subarctic Current, and 84.4% in the Transition Domain during August; and 88.1% in the Subarctic Current, 89.0% in the Transition Domain, and 99.2% in the Subtropic Region in September–October. Overall, the saury comprised 69.7% of the total weight of stomach contents.

The prevalence of Pacific sauries among total stomach content weights from June to September–October increased with decreasing latitude: 30.1% in the Alaskan Stream (one bird), 30.6% in the Subarctic Current, 79.9% in the Transition Domain, and 92.0% in the Subtropic Region. Since Sooty Shearwaters also increased in abundance with

decreasing latitude (see below), the above results indicate that the occurrence of Sooty Shearwaters and Pacific sauries coincided in the areas studied.

5.5. The importance of cephalopods

Precisely how long cephalopod beaks stay in a bird's gizzard is not known, but their presence indicates that the birds fed on cephalopods in the recent past. Both fresh and worn beaks were found in this study (Table 6). The maximum number of beaks in a single bird was 290 at station Ho9730 in the Transition Domain during July. Based on the frequency of occurrence of beaks in each oceanographic area regardless of month, squid decreased in importance as prey with decreasing latitude: 100% in the Alaskan Stream ($n = 1$ stomach) and Subarctic Current ($n = 48$), 66.7% in the Transition Domain ($n = 102$), and 43.5% in the Subtropic Region ($n = 22$) (Table 6). The same decreasing order was also observed in the average number of beaks per bird: 67.2 in the Subarctic Current, 40.3 in the Transition Domain, and 16.0 in the Subtropic Region. However, the number of beaks per bird between months did not show a trend. When all areas and seasons are combined, the frequency of squid beaks and the average number of beaks per bird are 72.8 and 48.6, respectively (Table 6). When compared with other seabirds in the same area such as Common Murres, Thick-billed Murres, and Short-tailed Shearwaters, Sooty Shearwater gizzards contained more cephalopod beaks (Ogi, unpubl. data).

The large number of squid beaks in gizzards suggests a greater use of these prey than indicated by stomach contents analysis. Squid comprised only 7.3% of the total food by weight, although they accounted 72.8% by frequency of occurrence (Tables 1 and 6). It appears that cephalopods are digested much faster than other large prey, which causes problems in the quantitative analysis of seabird food. Furthermore, some tiny hard beaks may have come from cephalopods inhabiting waters farther south; though most beaks came from squid, the few *Japetella* and *Argonauta* beaks were probably from prey eaten south of the Subarctic Boundary (Kubodera 1982). Nevertheless, the large number of beaks found in the gizzard indicate that the Sooty Shearwater depends considerably on small cephalopods in some localities during some periods. Judging from beak

Table 4
Frequency of occurrence, by month and area, of Pacific saury in the stomachs of the Sooty Shearwater; N = the number of stomachs, n = the number of stomachs in which the Pacific saury occurred, $\%[(n/N) \times 100]$ = the percentage occurrence

	Alaskan Stream			Subarctic Current			Transition Domain			Subtropic Region			Total		
Month	N	n	(%)	N	n	(%)	N	n	(%)	N	n	(%)	N	n	(%)
Jun.	—	—	—	8	0	(0)	30	10	(33.3)	13	5	(38.5)	51	15	(29.4)
Jul.	—	—	—	8	0	(0)	42	2	(4.8)	—	—	—	50	2	(4.0)
Aug.	1	1	(100)	28	4	(14.3)	6	4	(66.7)	—	—	—	35	9	(25.7)
Sep.–Oct.	—	—	—	4	1	(25)	24	8	(33.3)	9	6	(66.7)	37	15	(40.5)
Total	1	1	(100)	48	5	(10.4)	102	24	(23.5)	22	11	(50.0)	173	41	(23.7)

Table 5
Percentage by weight of Pacific saury in the stomach contents of the Sooty Shearwater by month and area; W = the total stomach content weight, w = the weight of the Pacific saury, $\%[(w/W) \times 100]$ = the percentage by weight

	Alaskan Stream			Subarctic Current			Transition Domain			Subtropic Region			Total		
Month	W	w	(%)	W	w	(%)	W	w	(%)	W	w	(%)	W	w	(%)
Jun.	—	—	—	49.731	0	(0)	491.490	433.011	(88.1)	98.853	77.255	(78.2)	640.074	510.256	(79.7)
Jul.	—	—	—	156.020	0	(0)	107.241	28.493	(26.6)	—	—	—	263.261	28.493	(10.8)
Aug.	35.070	10.571	(30.1)	56.155	35.299	(62.9)	33.718	28.456	(84.4)	—	—	—	124.943	74.326	(59.5)
Sep.–Oct.	—	—	—	76.797	68.229	(88.1)	173.544	154.368	(89.0)	189.686	188.097	(99.2)	440.027	410.694	(93.3)
Total	35.070	10.571	(30.1)	338.703	103.528	(30.6)	805.993	644.318	(79.9)	288.539	265.352	(92.0)	1468.305	1023.796	(69.7)

Table 6
The number of cephalopod beaks in Sooty Shearwater stomachs, by month and area; N = the number of stomachs, n = the number of stomachs in which cephalopod beaks occurred, $\%[(n/N) \times 100]$ = the percentage occurrence of cephalopod beaks

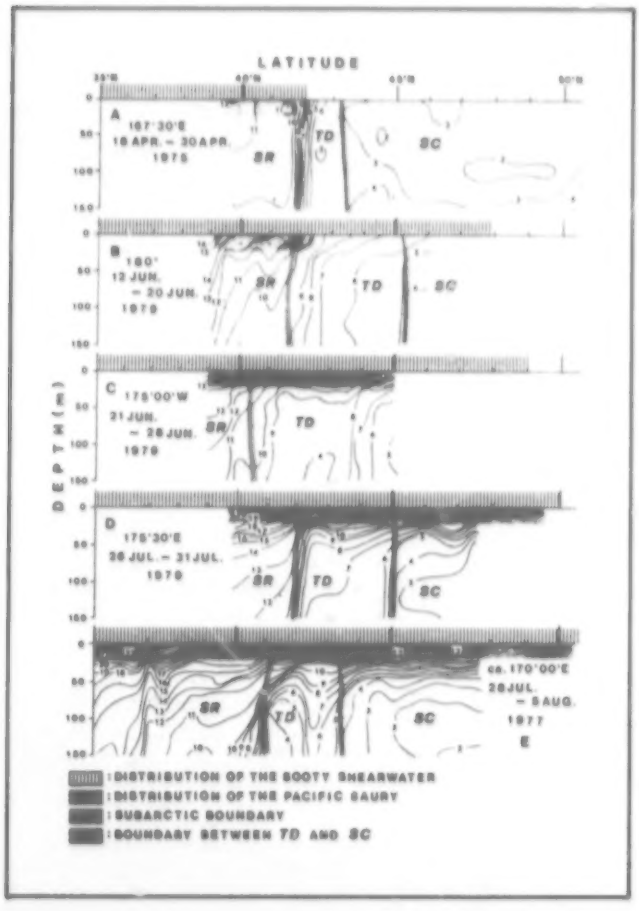
	Alaskan Stream				Subarctic Current					Transition Domain					Subtropic Region					Total				
Month	N	n	%	Mean	N	n	%	Range	Mean	N	n	%	Range	Mean	N	n	%	Range	Mean	N	n	%	Range	Mean
Jun.	—	—	—	—	8	8	100	37–171	76.8	30	7	23.3	1– 68	12.7	13	3	23.1	7–24	14.0	51	18	35.3	1–171	41.4
Jul.	—	—	—	—	8	8	100	.0–197	54.8	42	36	85.7	1–290	55.8	—	—	—	—	—	50	44	88.0	1–290	55.6
Aug.	1	1	100	8	28	28	100	2–273	75.0	6	3	50.0	1– 2	1.3	—	—	—	—	—	35	32	88.6	1–273	66.0
Sep.–Oct.	—	—	—	—	4	4	100	9– 32	19.0	24	22	91.7	2–116	29.1	9	6	66.7	8–32	17.0	37	32	86.5	2–116	25.6
Total	1	1	100	8	48	48	100	2–273	67.2	102	68	66.7	1–290	40.3	22	9	40.9	7–32	16.0	173	126	72.8	1–290	48.6

sizes, the original dorsal mantle lengths of most cephalopods probably ranged from 30 to 40 mm but some were as large as 250 mm (Kubodera, pers. comm.).

5.6. The occurrence of Sooty Shearwaters in relation to Pacific sauries and the oceanographic environment

Several seasons of systematically gathered transect counts of Sooty Shearwaters (Ogi, unpubl. data), along with concurrent data on Pacific sauries and shearwaters at gill-net fishing stations (Ogi, unpubl. data), and independently gathered information on Pacific sauries in various data records (Hokkaido Univ. 1979, 1980, 1981, and 1982) and the literature (Hotta and Fukushima 1970, Odate 1977, Fukushima 1979, Mishima *et al.* 1981), indicate that latitudinal movements of these two organisms in the North Pacific may be strongly affected by seasonal changes in the oceanographic climate. This was evident when the distribution of these two vertebrates were compared (Fig. 2) with the seasonal changes in the sea surface temperatures (SST).

Figure 2
Seasonal water temperatures by depth (isotherms in degrees Celsius), and occurrence of the Sooty Shearwater and Pacific saury. The position of the Subarctic Boundary coincided with the subsurface occurrence of 34 ‰ isohaline (Dodimead *et al.* 1963), and the boundary between the Transition Domain and the Subarctic Current coincided with the 4°C isotherm below 100 m (Favorite *et al.* 1976). SR: Subtropic Region; TD: Transition Domain; SC: Subarctic Current



Though temperatures optimal for the Pacific saury change seasonally with various stages of growth and migration, the fish was observed at SSTs ranging from 7 to 25°C; the most favourable fishing occurs at 14–18°C (Hotta and Fukushima 1970, Odate 1977). Thus, the northern distributional limit of the fish is assumed here to coincide with the 7°C isotherm, though the bulk of the population occurs farther south. Also to be considered in delineating the distribution of the Pacific saury, however, are the facts that larger fish (over 29 cm standard length) migrate farther north than smaller ones (Odate 1977) and that the frequency of occurrence of dense schools changes seasonally with SST as follows: 8.5–13.5°C (mode: 10.5°C) in June; 8.5–14.5°C (mode 12.5°C) in July; 10.5–16.5°C (mode: 11.5°C) in August; and 9.5–18.5°C (modes: 11.5, 14.5, and 17.5°C) in September (Odate 1977). These facts were taken into account for the preparation of Fig. 2.

Concurrent seabird censuses and gill-net fishing along long. 167°30′E from lat. 38°N to lat. 50°N during April indicated that both Pacific sauries and Sooty Shearwaters occurred just south of the Subarctic Boundary (Fig. 2A). At that time SSTs in adjacent sub-tropical and subarctic waters were 10.9–12.1°C and 2.2–4.2°C, respectively (Hokkaido Univ. 1976). By May the 7°C isotherm had reached the middle of the Transition Domain, and during this month both sauries and shearwaters crossed the Subarctic Boundary into the Transition Domain. By mid June at long. 180°, Sooty Shearwaters reached lat. 48°N in the Subarctic Current (Fig. 2B), but the 7°C isotherm reached only lat. 44°30′N near the northern edge of the Transition Domain (Hokkaido Univ. 1980). In fact, sauries were not then found in stomachs of sooties taken in the northern Transition Domain ($N = 30$) and Subarctic Current ($N = 3$). By July along long. 175°W, sauries entered the southern Subarctic Current (Hokkaido Univ. 1980: Fig. 2C). Sooty Shearwaters continued to occur yet farther north, some reaching the Alaskan Stream. From late July to early August, shearwaters and sauries occurred longitudinally across the Transition Domain, Subarctic Current, and Alaskan Stream (Hokkaido Univ. 1978, 1980: Fig. 2D and E). Along long. 175°30′E (Fig. 2D), Sooty Shearwaters reached north to lat. 50°N and sauries reached lat. 49°N, with schools occurring most frequently farther south in the northern Transition Domain (Hokkaido Univ. 1980).

6. Discussion

Dense feeding flocks of Sooty Shearwaters often occur where surface water temperatures range from 9 to 13°C in the North Pacific during summer, and compared with the similar Short-tailed Shearwater the sooty appears to prefer warmer waters (Ogi, unpubl. data). Its initial crossing of the Subarctic Boundary corresponds with the warming of surface waters beginning early in May. After this initial northward movement, lasting over a period of 1.5 months, its occurrence in the northern North Pacific is likely to be affected strongly by the occurrence and availability of suitable prey.

Sooty Shearwaters did not show changes in diet composition between oceanographic areas (as did *P. tenuirostris*, Ogi *et al.* 1980), but did show changes in diet by latitude: sauries decreased and squid increased with increasing latitude. In the overall diet, fish ranked highest by weight (83.1%), and the Pacific saury occupied 84% of this total fish weight. Weight of squid, however, was probably under-

estimated due to much more rapid digestion. The opposite trends with latitude shown by the prevalence of sauries and squid as Sooty Shearwater prey indicate that in the absence of this fish, squid was the dominant food. In the absence of both, the shearwater ate barnacles and jellyfish. It did not eat euphausiids which are important prey in upwelling areas closer to shore (Baltz and Morejohn 1977, Morejohn *et al.* 1978, Brown *et al.* 1981).

The periods during which the shearwater and the saury occur in the subarctic North Pacific coincided, and both species seemed to prefer 9–13°C temperatures (Odate 1977, this study). This may indicate that the distribution of this bird in the region may be related to water temperature, the occurrence of saury shoals, or both. The fact that shearwaters moved northward slightly ahead of the fish indicates that both organisms may be responding to temperature rather than the shearwater to the fish. Flying is a much more rapid means of dispersal than swimming. The additional fact that the importance of sauries as prey changed seasonally, but squid did not, suggests that the large-scale occurrence of the shearwater was a response to temperature whereas its smaller-scale occurrence related to prey availability.

In the present study, averaging observations from different sets of data and years served to indicate that an interesting interrelationship does exist between bird, prey, and sea surface temperature, but for this relationship to be properly understood, additional data will have to be gathered simultaneously.

7. Acknowledgements

I am grateful to G.A. Sanger and D.G. Ainley for their helpful discussion, reading, and criticism of the manuscript.

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A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska

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1. Abstract

We compared the diet and foraging distribution of five species of seabirds nesting at the two largest Pribilof Islands, which differ in the distribution of water masses around each island. We report significant asymmetry in the distribution of birds on the water around the islands. We also report significant differences in diet between members of the same species on the two islands, which are less than 100 km apart. In most cases, differences in volume of prey per bird were due to differences in the proportion of birds taking a prey, rather than due to differences in volume or number of prey per successful bird. The Walleye Pollock (*Theragra chalcogramma*) was taken by a higher proportion of birds on St. Paul than on St. George. A higher proportion of euphausiids was taken by birds on St. George than on St. Paul. The diets of breeding seabirds depended on the location of a colony in a physically heterogeneous ocean.

2. Résumé

Nous avons comparé le régime alimentaire et la répartition des aires d'alimentation de cinq espèces d'oiseaux de mer nichant dans les deux plus grandes îles Pribilof dont la distribution des masses d'eau entourant chaque île diffère. Il existe une importante asymétrie dans la distribution des oiseaux posés sur l'eau autour des îles. Nous signalons également l'existence de profondes différences dans le régime alimentaire de certains membres de la même espèce nichant dans les deux îles distantes de moins de 100 km. Dans la plupart des cas, les différences dans le volume de la proie par oiseau sont attribuables à des différences dans la proportion d'oiseaux qui capturent une proie plutôt qu'à des différences dans le volume ou le nombre de proies par oiseau opportuniste. La morue du Pacifique occidental (*Theragra chalcogramma*) est capturée par une plus forte proportion d'oiseaux sur l'île St. Paul. Toutefois, les euphausiidés sont capturés en plus grand nombre sur l'île St. George. Durant la saison de reproduction, les régimes alimentaires des oiseaux sont tributaires de la dispersion d'une colonie dans un océan physiquement hétérogène.

3. Introduction

During the breeding season most seabirds must find food in limited areas around breeding colonies, and must bring food back to colonies at sufficiently short intervals to support adequate growth of chicks. Previous studies of the diets of breeding seabirds have shown that the species at any one colony differ in prey selection, with somewhat greater differentiation of diets among species at tropical colonies (Ashmole 1968) than among species at higher latitude colonies (Pearson 1968, Hunt *et al.* 1980). Differences in diet have been attributed to foraging technique (Bédard 1969) and to interspecific variation in foraging range (Pearson 1968, Prince 1980, Croxall and Prince 1980). There have been few attempts to relate seabird diets to biologically significant features of the waters around colonies, although some comparisons of diet have been made for non-breeding birds at different locations (Hartley and Fisher 1936, Bradstreet 1980).

We here compare the foraging distribution and diets of seabirds at the two largest Pribilof Islands, which are surrounded by water masses that differ in ecologically significant ways. We describe the physical and biological environment, with an emphasis on those factors most likely to affect food distribution and foraging behaviour. We then show that significant differences in diet exist at a scale of less than 100 km, despite large variation in volume, number, and types of prey taken by individual birds. We show that dietary heterogeneity between the two islands is due primarily to individual variation in the type of prey taken, rather than variation in the amount of each prey taken. Finally, we discuss our results in light of recent oceanographic studies in the southeast Bering Sea.

4. Physical and biological setting

The Pribilof Islands, located at the edge of a relatively wide continental shelf, are isolated from the nearest land by 330 km of open ocean (Fig. 1). St. George is the higher of the two large islands, with a cliff area of 3.5 km^2 along its perimeter (Hickey and Craighead 1977). St. Paul is lower and has a cliff area of 0.5 km^2 along its perimeter. St. Paul is located 100 km from the shelf break, whereas St. George is only 25 km from the shelf break. Associated with the shorter distance to the shelf break is a steeper gradient in bathymetry around St. George. As a result of differences in bathymetry and location, the islands differ in two oceanographic features: distance to a water mass boundary (inner front) associated with the 50-m isobath, and distance to another front at the shelf break.

During the summer, a vertically homogeneous water mass forms around both islands (Kinder *et al.*, in press). A thermocline forms in water deeper than about 50 m, but fails to form in shallower water because wind mixing reaches to a depth of 30 m, while tidal forces stir water upwards to 20 m off the bottom. Because mixing occurs down to the bottom, rather than just to a thermocline at

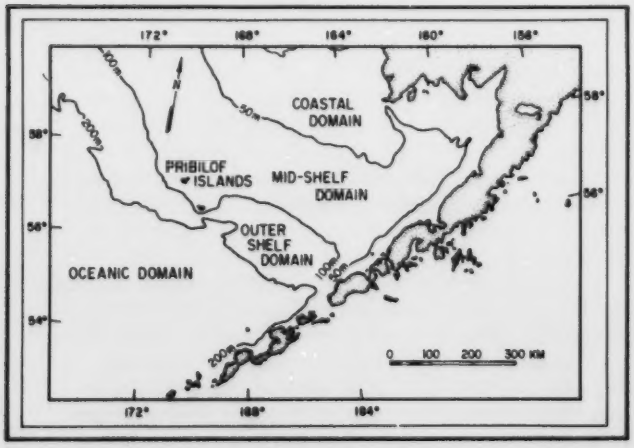
about 30 m, heating of surface water occurs more slowly in the homogeneous water mass around the island than in the stratified water offshore. Because of local bathymetry this water mass extends farther to the northeast than to the southwest of St. Paul, and it extends farther outward from St. Paul than from St. George. The front that marks the transition from stratified to well-mixed water around the islands is relatively sharp (Kinder *et al.*, in press). Enhanced vertical mixing occurs at similar fronts in other continental seas (Swallow *et al.* 1981, Simpson and Pingree 1978).

The two islands also differ in their proximity to a northwestward flowing boundary current at the shelf edge. This current is weak relative to other boundary currents (Kinder and Coachman 1978), but like other shelf-break currents at similar latitudes, this current is associated with a permanent front that marks the transition from shelf waters (less haline, greater seasonal variation in temperature) to oceanic waters (more haline, less seasonal variation in temperature). This front shelf break begins at the 170-m isobath (Fig. 1).

A third front lies shoreward of the shelf-break front east of the Pribilof Islands. This front is associated with the 100-m isobath (Coachman and Charnell 1979) and it marks the transition from a two-layer system over the mid-shelf zone, to a three-layer system over the outer shelf zone. This front has not been delineated from hydrographic data near the Pribilofs, but from bathymetric considerations, coastal (<50 m) and middle shelf (50–100 m) waters can be expected to the north of St. Paul Island (Fig. 1). Outer shelf waters (100–170 m) are limited to the area southeast and southwest of St. George Island (Iverson *et al.* 1979).

Little is known about the distribution of plankton and nekton in the immediate vicinity of the two islands. Studies of zooplankton (Motoda and Minoda 1974) and juvenile pollock (Smith 1981) suggest that higher standing stocks of these groups occur on the outer shelf (greater than 100-m depth) and hence are most abundant to the southwest of the Pribilof Islands. The outer shelf in the Bering Sea is dominated by a pelagic food web, whereas the middle shelf (roughly 50 to 100-m depth) is dominated by a benthic food web (Iverson *et al.* 1979, Schneider and Hunt 1982). It is thus likely that food available to birds is different around the two islands, because coastal or middle shelf waters extend north and northeast of St. Paul, whereas outer shelf waters cover much of the area to the south and southeast of St. George (Fig. 1).

Figure 1
Location of Pribilof Islands in the southeastern Bering Sea. St. Paul Island is to the north, and St. George Island is to the south



5. Methods

5.1. Data collection

Bird counts were made around the Pribilof Islands on cruises in July 1977, May 1978, August 1978, and September 1978. All bird counts were made while the ship was underway at speeds ranging from 10 to 20 km/h. All sitting birds in a sector extending to 300 m directly abeam of the vessel off the side with the best visibility were recorded during 10-min watches. Counts were standardized by excluding ship-following birds, and by dividing the count by the area scanned during each watch. Counts were made almost continuously during daylight hours, except during periods of fog. Cruise tracks were oriented along radii extending outward from both islands. For this analysis, only birds on the water were counted, as they were either observed to be feeding or were assumed to have been feeding recently in the area where they were seen.

Food samples were obtained from birds that were shot while they were returning to the island from sea. Birds were collected from a skiff within 2 km of land, or at points of land crossed by returning birds. Collections were made every 2–4 days. Collections were made throughout the day, but the majority of birds (60%) were collected during the 4-h period before noon, local time. Most of the collecting was done in June, July, and August 1975–78 (Table 1). Ethanol (70–80%) was injected down the esophagus to arrest digestion. Most carcasses were opened within 12 h of collection. All food in the proventriculus, gular pouch, and stomach was removed and placed in a plastic bag in 80% ethanol.

Samples were sorted in the laboratory by identifying each item to the lowest taxon possible, then recording displacement volume for each taxon. The number of items per taxon was estimated by counting identifiable parts (heads, eyes, beaks, or tails) and dividing by the number of such parts in an intact organism. This measure is a standing stock estimate, rather than a rate measurement (ingestion per unit time).

5.2. Data analyses

Analyses were confined to the five piscivorous bird species for which a statistically adequate sample was available on both islands. Only two stomachs were available for Red-faced Cormorants from St. George, so regurgitations were used in the analysis. A preliminary comparison of cormorant stomach and regurgitation samples collected on St. Paul Island, where our sample of stomachs was larger, showed that prey composition (% occurrence) did not differ significantly between the two methods of collection. Stomach samples were analysed for the four remaining species. Samples were pooled to provide adequate replication.

We designed statistical analyses to control problems that arose: differential digestion of prey taxa and the effects of high individual variation in diets when comparing the average numbers or volumes of prey in two or more groups.

The problem of differential digestion in analysing diets was controlled by making statistical comparisons within prey categories. The variance due to differential digestion among prey taxa is thus eliminated from the analysis, which

assumes only that digestion rates of any given prey are equal on the two islands. Two-sample ANOVAS were made on prey number and prey volume per bird, for any prey taxon that accounted for more than 5% of the number or volume of prey taken by St. Paul birds or by St. George birds.

If the average number or volume of prey per bird differed significantly between St. Paul and St. George, the analysis was carried further to see if the variation was due to differences in the proportion of birds taking a prey (percent occurrence of a prey taxon in the sample of birds) or whether the variation was due to differences in number or volume of prey taken by successful birds. G-tests (Sokal and Rohlf 1969) were used to test for differences in proportion (i.e. differences in % occurrence). Two-sample ANOVAS were used to test for differences in number or volume of a taxa per capture (i.e. birds without the prey taxa were excluded from the analysis). No test was performed if the sample size was zero for an island (no instances of capture). Criterion levels were set at a conservative level ($P = 0.01$) since a large number of tests were performed. If two samples were heteroscedastic (had unequal variances at $P = 0.01$), a non-pooled estimate of variance was used.

We divided the area around the islands into circumferential zones set at 20 km, 60 km, and 110 km from the islands (Fig. 2). Distances correspond roughly to major bathymetric features (50-m isobath, 100-m isobath, shelf break) that govern mixing regime and water mass distribution. If water masses are important, then the distribution of birds between these zones will be asymmetrical. Asymmetries in bird distribution were tested by comparing corresponding zones in the northeast and southwest (shelf-break) sides of the study area (Fig. 2).

Table 1
Food samples collected at the Pribilof Islands, 1975–78

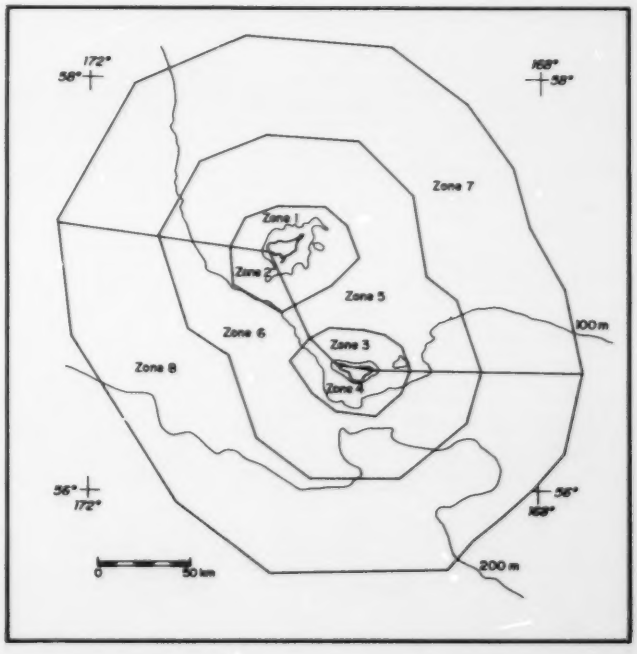
	St. Paul Island				St. George Island		
Species	**1975**	**1976**	**1977**	**1978**	**1976**	**1977**	**1978**
Red-faced Cormorant (regurgitations)							
June				1		5	1
July	14	19	7	6	6	17	8
August	17	12			14		1
September		1					
Totals	31	32	7	7	20	22	10
Black-legged Kittiwake (stomachs)							
April				3			
May			4	9		3	4
June	2		11	2		24	5
July	16	10	16	43	2	14	5
August	1	3	6	14	1		1
September	4					1	
Stomachs with food	23	13	37	71	3	42	15
Stomachs examined	27	21	48	74	3	56	46
Red-legged Kittiwake (stomachs)							
April						8	
May			1	10		1	12
June	1		1	5	1	28	8
July	1	7	22	26		3	1
August		2	12				1
September		21	3				
Stomachs with food	2	30	39	41	1	40	22
Stomachs examined	2	34	40	45	1	58	56
Common Murre (stomachs)							
April	1						
May				3			
June	5		5	2			3
July	9	14	1	25			
August	1	4	6	1		1	
September	6	1		1			
Stomachs with food	22	19	12	32		1	3
Stomachs examined	31	22	43	36		2	7
Thick-billed Murre (stomachs)							
May				1			
June	2	1	8			12	19
July	13	5	3	15	1	6	13
August		3	13	1		12	14
September	1						
Stomachs with food	16	9	24	17	1	30	46
Stomachs examined	22	15	35	25	1	36	71

6. Results

6.1. Colony composition

St. George Island has seven times the cliff area of St. Paul Island (Hickey and Craighead 1977). Population sizes of cliff-nesting species deviated strongly from this ratio. St. George harboured a disproportionate number of "pelagic" species, which have long flight ranges and which tend to be found in a few large colonies near deep water (Hunt *et al.* 1981*b*): Northern Fulmar (*Fulmarus glacialis*), Red-legged Kittiwake (*Rissa brevirostris*), and Thick-billed Murre (*Uria lomvia*). The ratio of these species between St. George and St. Paul was 100 to 1, 100 to 1, and 14 to 1 respectively (Sowls *et al.* 1978). St. Paul harboured a disproportionate number of more ubiquitous coastal nesters, found in small to intermediate colonies throughout the eastern Bering Sea: the Red-faced Cormorant (*Phalacrocorax urile*), Black-legged Kittiwake (*Rissa tridactyla*), and Common Murre (*Uria aalge*).

Figure 2
Zones used to analyse seabird abundance around the Pribilof Islands. The concentric rings are 20, 60, and 110 km from the nearest island



The ratios of these species between St. George and St. Paul were 2 to 1, 2 to 1, and 5 to 1 respectively (Sowls *et al.* 1978).

6.2. Distribution and diet

Foraging by Red-faced Cormorants was confined to within 20 km of the islands (Table 2). The highest densities of birds on the water (presumed to have recently fed) were observed northeast of St. Paul, an area of relatively shallow water. This species took a wide variety of prey: over 56 prey groups were identified in 127 samples. Benthic groups (shrimp, crabs, cottids, and other scorpaeniform fish) were the most important prey (Fig. 3). St. Paul birds took a greater proportion of shrimp than St. George birds (Fig. 4). Differences in the taking of shrimp were due to differences in the proportion of birds taking prey (Fig. 5). If analysis was restricted to those cormorants in which a given prey species was present, there were no significant differences at $P = 0.01$ between the two colonies in the average number or average volume of that prey species per bird. Differences in diet between populations on the two islands were due to the number of birds taking prey (Fig. 5), rather than how much a bird took.

Foraging by Common Murres occurred mostly within 60 km of the islands (Table 2). Density values are low because not all murres could be identified to species. Like the cormorant, Common Murres showed a consistent preference for the shallow waters in the northeast of the study area (Table 2). Diets differed significantly with respect to only one prey species: St. George birds contained a greater volume and number of euphausiids than St. Paul birds (Figs. 6 and 7). These differences were due to the proportion of birds taking a prey (Fig. 8). There were no significant differences in the volume of a prey taxon taken by successful birds between islands ($P = 0.01$). However, the small number of birds collected on St. George ($N = 4$) may not

Figure 3
Volume of prey in food samples of Red-faced Cormorants. Volume is expressed as a percentage of the total volume found in samples from one island. Solid bars indicate significant differences ($P = 0.01$) between islands

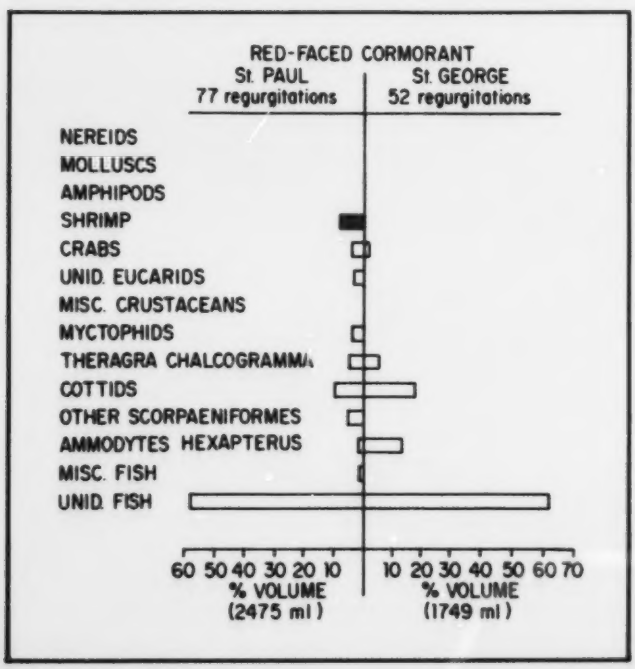


Figure 4
Number of prey in food samples of Red-faced Cormorants. Number is expressed as a percentage of the total number of items recorded in samples from one island. Solid bars indicate significant differences ($P = 0.01$) between islands

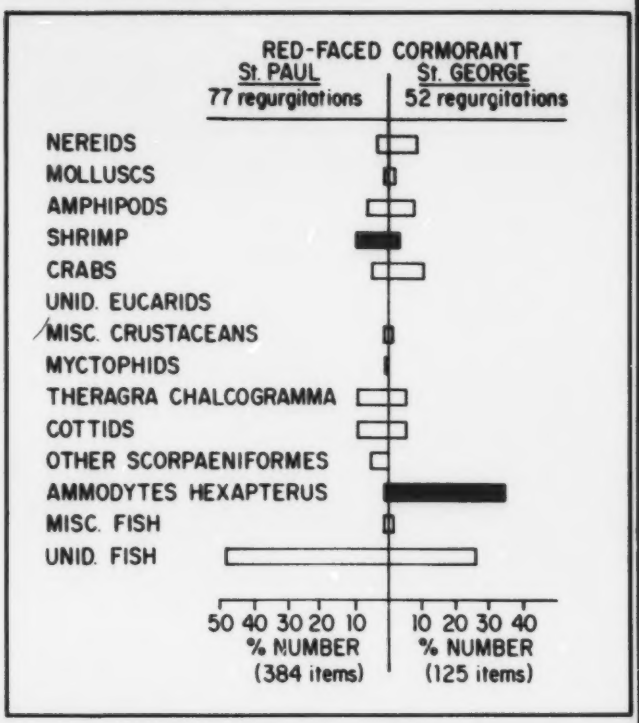
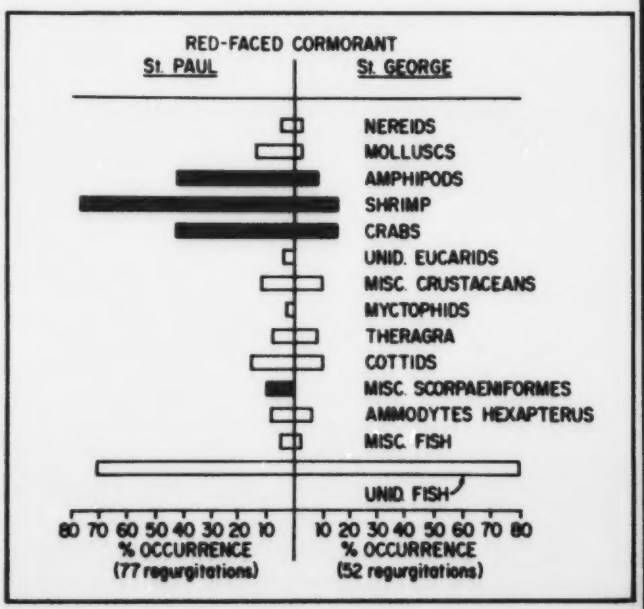


Figure 5
Occurrence of prey in food samples of Red-faced Cormorants. Occurrence is the percentage of samples with a prey, within each island. Solid bars indicate significant differences ($P = 0.01$) between islands



have been representative, although they were collected in different years (1976 and 1977) and months (June and July).

Black-legged Kittiwakes foraged at greater distances from the islands than Red-faced Cormorants or Common Murres, but like these species, Black-legged Kittiwakes showed a strong preference for shallow waters to the northeast of St. Paul (Zones 1, 5 and 7; Table 2). Walleye pollock (*Theragra chalcogramma*) was the most important prey species for Black-legged Kittiwakes and more were taken on St. Paul than St. George (Figs. 9 and 10). Observed differences between the two populations of Black-legged Kittiwakes were due to changes in the proportion of birds taking a prey (Fig. 11), rather than due to differences in number or volume taken by successful birds.

Thick-billed Murres foraged in considerable numbers in the most distant zones from the islands (Table 2), which agrees with the morphological analysis of Spring (1971) who demonstrated adaptations for long distance flight in *U. lomvia*. This species showed a preference for deeper water, based on relatively low densities of birds northeast of St. Paul Island (Zone 1; Table 2). Invertebrates formed a major part of the diet (Figs. 12 and 13). Differences between the islands were small (Figs. 12 and 13), although a significantly greater proportion of St. George birds took euphausiids (Fig. 14), and the proportion of all invertebrates to all fish was higher on St. George than on St. Paul. There were no differences in number or volume of a prey taxon taken by successful birds on the two islands ($P = 0.01$).

The Red-legged Kittiwake showed a strong preference for waters at or beyond the shelf break (Table 2).

Figure 6
Volume of prey in stomach samples of Common Murres. Solid bars: $P = 0.01$

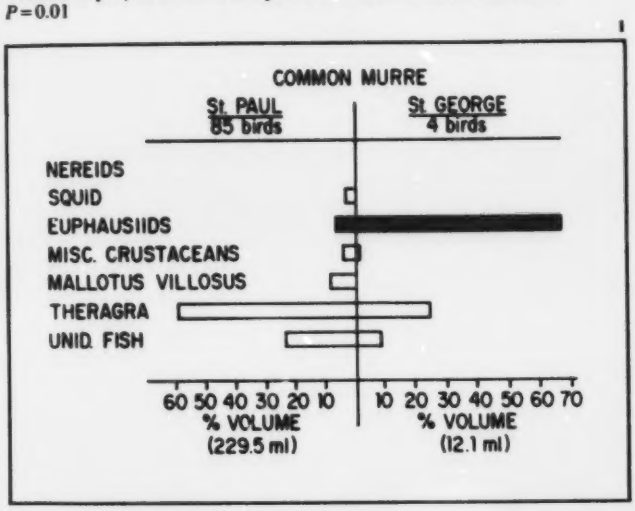


Figure 7
Number of prey in stomach samples of Common Murres. Solid bars: $P = 0.01$

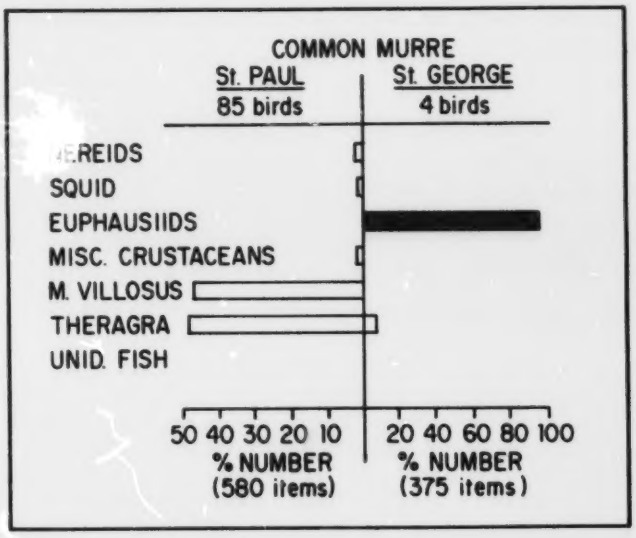


Table 2
Density of birds on the water (birds/km²) in eight zones around the Pribilof Islands. See Figure 2 for locations of zones

Distance			Red-faced Cormorant		Black-legged Kittiwake		Red-legged Kittiwake		Common Murre		Thick-billed Murre	
			NE	SW	NE	SW	NE	SW	NE	SW	NE	SW
20 km	St. Paul	Zone	1	2	1	2	1	2	1	2	1	2
		$\bar{X}$*	0.94	0.51	0.36	0.08	0.009	0.0	0.22	0.05	0.13	0.32
		SD†	4.92	1.78	1.83	0.34	0.14	0.0	1.05	0.25	0.58	0.88
		N‡	217	74	217	74	217	74	217	74	217	74
	St. George	Zone	3	4	3	4	3	4	3	4	3	4
		$\bar{X}$	0.45	0.18	0.12	0.21	0.02	0.03	0.21	0.02	0.70	0.64
		SD	1.79	0.90	0.46	1.28	0.18	0.21	1.06	0.12	2.81	2.83
		N	119	172	120	172	120	172	120	172	120	172
60 km		Zone	5	6	5	6	5	6	5	6	5	6
		$\bar{X}$	0.005	0.008	0.32	0.16	0.06	0.30	0.18	0.15	0.53	0.27
		SD	0.09	0.13	1.66	1.09	0.45	3.06	0.69	0.86	1.68	0.97
		N	357	297	357	297	357	297	357	297	357	297
110 km		Zone	7	8	7	8	7	8	7	8	7	8
		$\bar{X}$	0.003	0.0	0.22	0.13	0.0	0.30	0.06	0.009	0.22	0.35
		SD	0.06	0.0	1.62	0.99	0.0	3.99	0.34	0.12	0.90	2.52
		N	298	437	298	437	298	437	298	437	298	437

*$\bar{X}$ = average number of birds/km².
†SD = standard deviation.
‡N = number of transects.

Myctophids, a deep-water fish, were the principal prey (Figs. 15 and 16). There were no significant differences between colonies in the proportions of birds taking this prey (Fig. 17) but there were significant differences in the average number of myctophids per bird (Fig. 16). The number of myctophids per successful bird also differed significantly between St. Paul birds (6.5 fish per successful bird) and St. George birds (4.25 fish per successful bird). Volume of myctophids per bird (Fig. 15) did not differ significantly between the two islands, nor did volume per successful bird ($P = 0.01$).

Figure 8
Occurrence of prey in stomach samples of Common Murres. Solid bars: $P = 0.01$

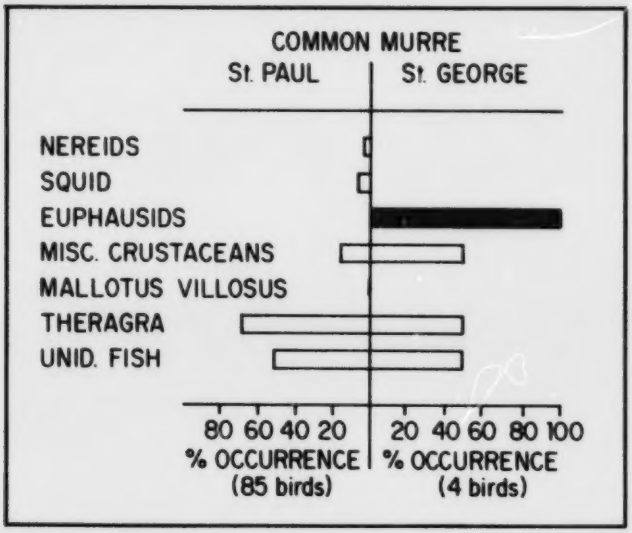
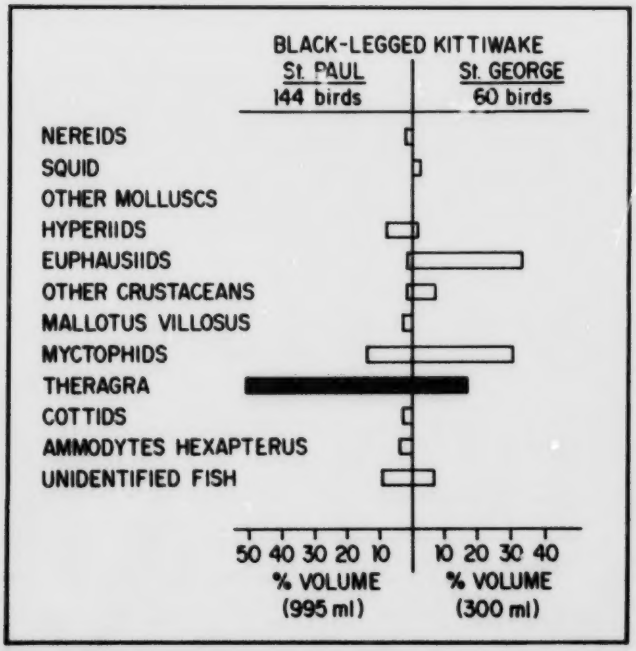


Figure 9
Volume of prey in stomach samples of Black-legged Kittiwakes. Solid bars: $P = 0.01$



7. Discussion

This comparative analysis of two seabird colonies demonstrated that (1) the distribution of birds foraging around breeding colonies can vary with local oceanographic differences; and (2) diets can differ significantly between populations of the same species on nearby colonies located in different oceanographic environments.

Figure 10
Number of prey in stomach samples of Black-legged Kittiwakes. Solid bars: $P = 0.01$

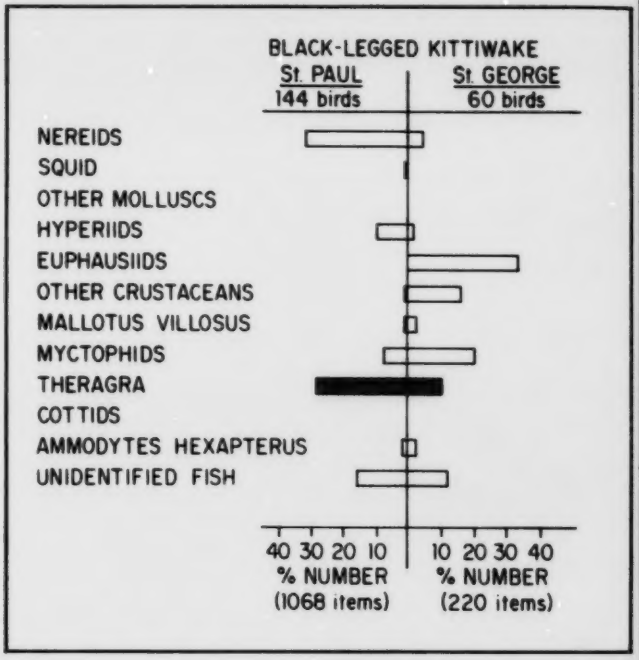
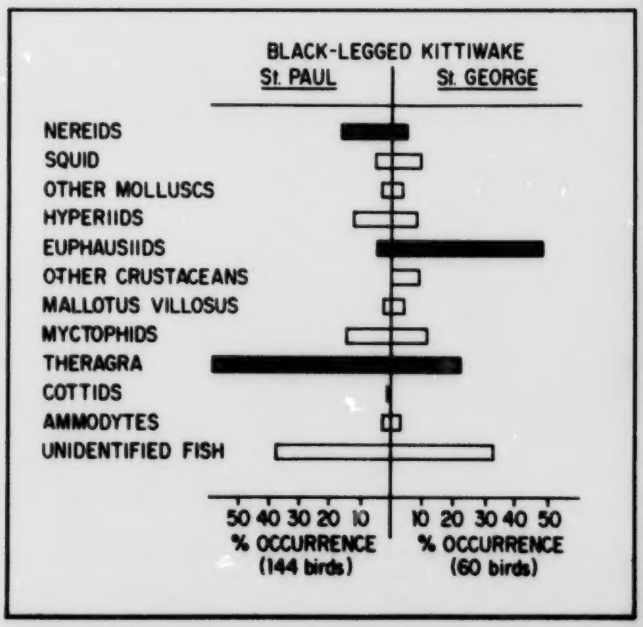


Figure 11
Occurrence of prey in stomach samples of Black-legged Kittiwakes. Solid bars: $P = 0.01$



Previous ideas on foraging distribution around breeding colonies have been from inference only (Pearson 1968, Ashmole and Ashmole 1967, Croxall and Prince 1980) and from scattered observations at sea (Cody 1974, Ashmole and Ashmole 1967). Foraging distribution as a function of distance from the colony was modelled by Cody (1974) who predicted species replacement along radii extending outward from a colony. Cody's own data failed to support the model (Bédard 1976) and radial replacement of predators could result from radial replacement of prey, rather than optimal return rates as a function of predator size and flight range as predicted by Cody. The asymmetrical distribution of birds around the Pribilof Islands indicates that foraging distribution is not related entirely to distance. Prey type and availability is likely to be related to both distance and direction, and prey distribution will need to be included in any realistic model of seabird foraging.

Analyses of diet relative to oceanographic conditions include those of Bradstreet (1980) and Hartley and Fisher (1936) (see also Briggs *et al.*, this volume), who collected foraging birds from different habitats. Bradstreet found that alcids feeding at onshore ice-edges took different proportions of prey from birds feeding at offshore ice-edges. Hartley and Fisher found that euphausiids were taken by most birds feeding in waters at the foot of a glacier, whereas amphipods appeared in the diets of birds feeding in waters affected by stream runoff. Local variation in diets of breeding seabirds has been reported by Uspenski (1958) and Belopolskii (1957), but no attempt was made to relate these differences to local oceanographic conditions.

Figure 12
Volume of prey in stomach samples of Thick-billed Murres

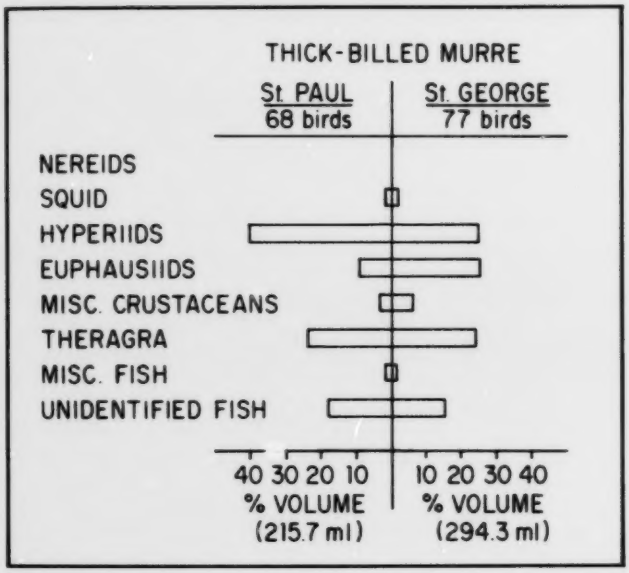


Figure 13
Number of prey in stomach samples of Thick-billed Murres

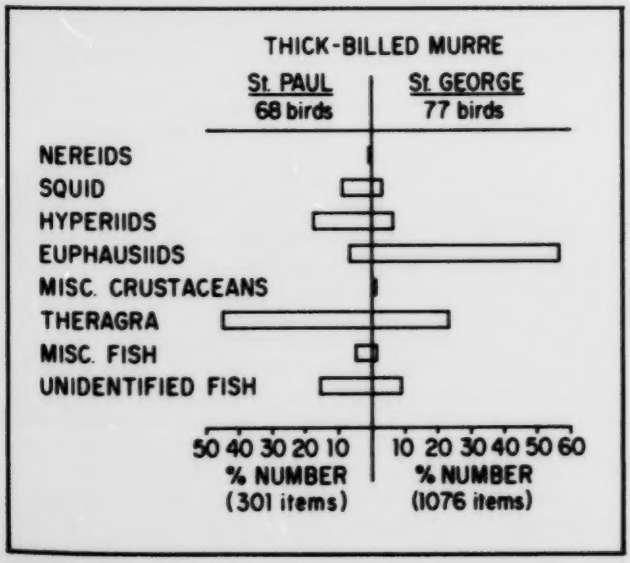


Figure 14
Occurrence of prey in stomach samples of Thick-billed Murres. Solid bars: $P = 0.01$

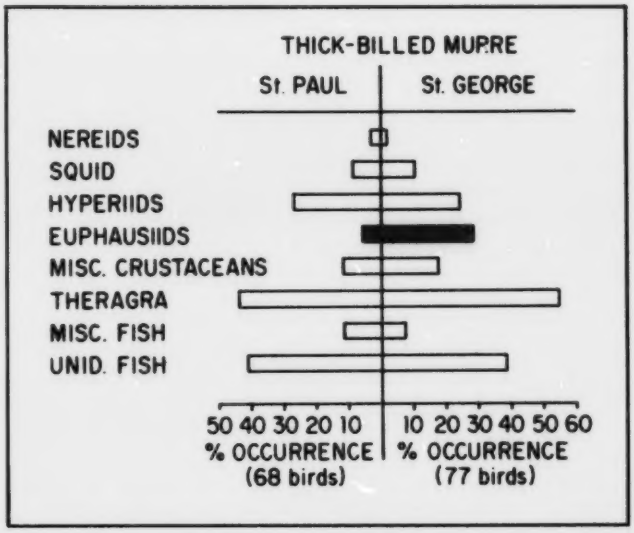


Figure 15
Volume of prey in stomach samples of Red-legged Kittiwakes. Solid bars: $P = 0.01$

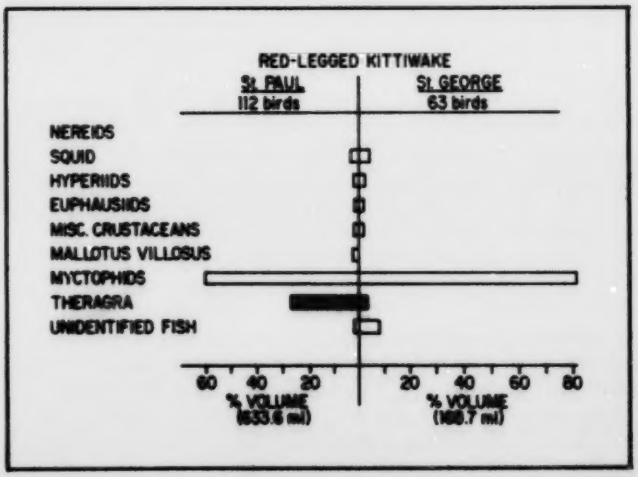


Figure 16
Number of prey items in stomach samples of Red-legged Kittiwakes. Solid bars: $P = 0.01$

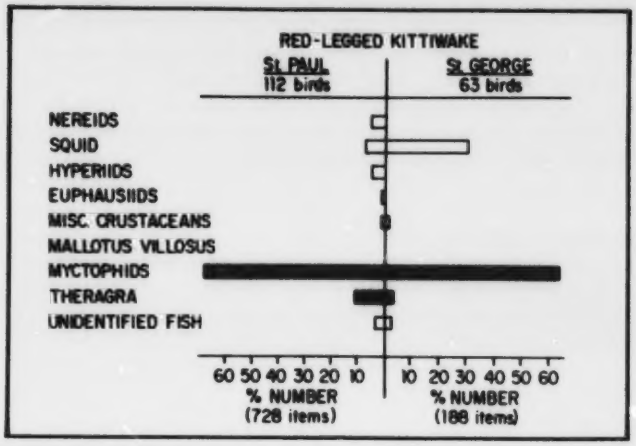
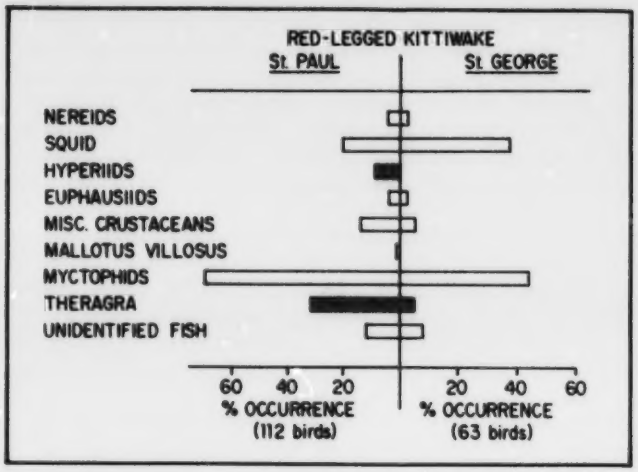


Figure 17
Occurrence of prey in stomach samples of Red-legged Kittiwakes. Solid bars: $P = 0.01$



Comparison of the two Pribilof colonies suggests that habitat selection occurred relative to oceanographic features that influence productivity and transfer of energy through the food web. Two of the three coastal species (Common Murre and Red-faced Cormorant) were found predominantly on shallow waters to the northeast of the Pribilofs (Table 2), waters with the same mixing regimes found in the coastal and middle shelf domains in the southeastern Bering Sea (Kinder *et al.*, in press). The third species common in coastal colonies, the Black-legged Kittiwake, was found at greater distances from the island than Common Murres and Red-faced Cormorants, but like these two, Black-legged Kittiwakes were most often found on the relatively shallow waters extending to the northeast of the islands, except in the immediate vicinity of St. George Island (Table 2). Thus, elements of these three populations on the Pribilofs used the islands as if they were a coastal site. In contrast, Red-legged Kittiwakes concentrated their foraging in deep waters well offshore (Table 2). This pattern of habitat selection gives this predator access to a prey group (myctophids) that were taken throughout the breeding season, unlike pollock. Myctophids were abundant dietary items from May to September, whereas pollock were taken primarily in July (Hunt *et al.* 1980).

Wiens *et al.* (1978) estimated that energy flux near the St. George breeding colony was 18 times greater than energy flux near the St. Paul colony. Much of this difference was due to the large populations of Thick-billed Murres and Northern Fulmars on St. George. The ability of these two species to obtain significant proportions of their diet near the shelf break may be critical for supporting the large populations on St. George Island. Large-bodied zooplankton (*Neocalanus cristatus*, *N. plumchrus*, and *Eucalanus bungii*) appear to be a key link in the food chain. High standing stocks of these species (7–180 g wet weight/m^2) occurred along the outer part of the continental shelf in three successive years relative to those in the coastal and middle domain waters (Cooney 1981). These species overwinter at depth as adults, and rise to the surface in the spring to take advantage of the spring phytoplankton bloom. Large copepods are the major prey of juvenile pollock (Clarke 1978) when these fish reach the size range taken by seabirds (Hunt *et al.* 1981*a*). Spawning pollock concentrate along the outer shelf and juveniles appear to concentrate in the region of the Pribilof Islands before dispersing outwards across the shelf (Smith 1981).

One feature of the diets of seabirds on the Pribilof Islands is the paucity of surface schooling fish, such as *Ammodytes* or osmerids. The near absence of these fish in the diets of seabirds at the Pribilofs suggest that these shallow water fish are not abundant around the Pribilof Islands. The two major prey groups at the Pribilofs are a demersal fish (walleye pollock), and species that migrate vertically (myctophid fish and euphausiids). Pollock are important prey on both islands, while the vertical migrants are more important on St. George. Vertical migration may be an important mechanism bringing food to the surface in deep waters south of the islands, while shallow waters may be important in making food accessible to diving birds around the islands and to the north of St. Paul. Ashmole and Ashmole (1967) noted the importance of vertically migrating prey in the ecology of seabirds breeding on oceanic islands in the tropics. Factors that govern vertical migration of nekton may prove to be a major factor in the lives of oceanic, as opposed to coastal breeding seabirds.

Our knowledge of the hydrography of the southeastern Bering Sea has advanced rapidly in the last decade, largely as a result of work sponsored by the Outer Continental Shelf Environmental Assessment Program (National Oceanographic and Atmospheric Administration) and PROBES (Processes and Resources of the Bering Shelf Ecosystem). The concept of a current flowing northward across the shelf, fed by a net influx of North Pacific water through the Aleutian passes, has been replaced by the concept of well differentiated water masses that undergo little net advection, though they oscillate with the tide (Coachman and Charnell 1979, Kinder and Schumacher 1981). The lack of net advection across the shelf in the southeastern Bering Sea has a number of important biological consequences. First, the physical characteristics of the water inhabited by marine life is conditioned by local forces, including heating by the sun, stirring and mixing by the wind and tidal action. Second, critical nutrients such as silicate, nitrates, and phosphates are not replenished by water from elsewhere. Third, there is little opportunity for lateral transport of biological populations.

Understanding of the biological oceanography of the region is still in a state of flux, but at present it is clear that there is an abrupt change in species composition across the shelf, and that this change coincides with the middle front, which is associated with the 100-m isobath. There are differences in population density on either side of the 100-m isobath for several species of zooplankton (Cooney 1981), fish (Bakkala *et al.* 1979), benthos (Haflinger 1981), and birds (Hunt *et al.* 1981*c*). Differences in biomass have been reported in several ecological assemblages, most notably chain-forming diatoms (Goering and Iverson 1981), deposit-feeding infauna (Haflinger 1981) large-bodied copepods (Cooney 1981), and surface-feeding birds (Schneider and Hunt 1982).

Differences in species composition on either side of fronts between water masses are well documented for marine ecosystems. Differences in population density of various organisms on either side of fronts have been reported for the southeastern Bering Sea (Iverson *et al.* 1979), the North Sea (Joiris 1978), and the Sargasso Sea (Backus *et al.* 1969). The association between marine birds and water masses is well documented, beginning with the work of Murphy (1936) and extending to the finer scale analyses of Brown *et al.* (1975) and Pocklington (1979). The asymmetrical distribution of birds around the Pribilof Islands extends this result to the distribution of birds around breeding colonies.

Although the association between marine populations and water masses is well known, the underlying mechanisms are not. In the North Sea, Joiris (1978) emphasized differences in algal mortality and bacterial activity in adjacent water masses. In the Bering Sea, Cooney (1981), Goering and Iverson (1981), Iverson *et al.* (1979), and Schneider and Hunt (1982) emphasized differential grazing pressure due to the ontogenetic migration of large-bodied zooplankton into surface waters of the outer shelf during the spring bloom. These zooplankton may supply food to surface-feeding birds either directly (storm-petrels) or indirectly through squid and fish (Fulmars and Red-legged Kittiwakes). Lower grazing pressure over the middle shelf allows more phytoplankton to sink to the bottom to feed benthic detritivores and their predators (Haflinger 1981). An important but untested aspect of this hypothesis is that the lateral (especially shoreward) movement of large-bodied zooplankton is limited by the fronts, despite the mobility of these animals. The hypothesis does not account for distribution of diving birds, most notably the large biomass of murres in the outer domain near the Pribilof Islands.

Recent work suggests that some of the mechanisms responsible for the association between marine populations and water masses may be acting at small spatial scales. Cooney (1981) showed that the biomass of large-bodied copepods is high near the shelf-break front, and decreases across the outer shelf domain toward land. Seabirds aggregate at both the shelf break and the inner fronts in Bristol Bay (Schneider 1982), and significant aggregations of murres associate with fronts around the Pribilof Islands (Kinder *et al.* 1983). Seabirds need to be examined relative to large- and small-scale physical and biological phenomena to understand the trophic processes that link them to marine ecosystems.

In summary, the two Pribilof colonies differed in colony composition, diet of individual species, and distribution of birds around the colony. An understanding of the physical factors that influence marine food webs suggests that these differences between the two colonies are a function of the heterogeneous ocean that surrounds the colonies.

8. Acknowledgements

We thank the following people for help with identification of prey: A. Adams (myctophids), T. Bowman (amphipods), G. Brusca, B. Burgeson, D. Causey, R. Cimberg, T. Cooney, K. Coyle (amphipods), K. Fauchald (polychaetes), J. Fitch, A. Fleminger (copepods), K. Frost (fish), E. Hall (fish), E. Hochberg, K. Hulsemann, B. Mayer, G. Mueller, J. Quast, G. Sanger, N. Wicksten (shrimp), R. Winn, and R. Wolotira.

We thank B. Braun, Z. Eppley, B. Mayer, M. Naughton, W. Rodstrom, D. Siegel-Causey, R. Squibb, and D. Schwartz for help in the field, M. Warner for setting up the studies on the Pribilof Islands, and the National Marine Fisheries Service, St. Paul Island, for logistic help.

We thank G. Bush, Z. Eppley, J. Mershman, and C. Wallace for getting the data into the computer, and W. Johnson, H. Peterson, and K. Watts for help in getting the data out of the computer.

Thanks go to P. McDonald and C. Nicklin for typing the manuscript, and to D. Ainley, D. Duffy, Z. Eppley, P. Gould, C.P. McRoy, G. Sanger and an anonymous referee for commenting on the manuscript.

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Fish changes in diets of nestling Rhinoceros Auklets and their implications

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1. Abstract

The diet of nestling Rhinoceros Auklets (*Cerorhinca monocerata*) was investigated on offshore Triangle Island (1976–79) and on inshore Pine Island (1977–80) and Lucy Island (1979–80), British Columbia. Variations in the diet occurred between years and within each summer. The annual variations include the early predominance of Pacific sauries (*Cololabis saira*) in 1976, fluctuations in abundance of age groups of Pacific sandlance (*Ammodytes hexapterus*) and Pacific herring (*Clupea harengus*), a change in rockfish (*Sebastes*) species, and the appearance of bathypelagic bluethroat argentines (*Nansenia candida*) in 1978. In a given summer sandlance and rockfish predominated in July, and herring and sauries in August. Changes in age and size of sandlance species, composition of rockfish, and occurrence of sauries and bluethroat argentines at Triangle and Pine islands were synchronized over the years. Sauries were more prevalent in the diet of birds feeding in the offshore waters of Triangle Island, whereas herring was more prevalent at inshore Pine and Lucy islands.

Juvenile fish populations in surface waters are very difficult to study by conventional methods of pelagic sampling. The Rhinoceros Auklet diet, together with complementary net studies, provides a means of sampling populations and monitoring age-classes of juvenile fish.

2. Résumé

Nous avons étudié le régime alimentaire de jeunes Alques à bec cornu (*Cerorhinca monocerata*) dans l'île hauturière Triangle (1976 à 1979) et dans les îles côtières Pine (1977 à 1980) et Lucy (1979 et 1980) en Colombie-Britannique. Les variations du régime alimentaire se manifestent d'une année à l'autre et au cours de chaque été. Pour ce qui est des variations annuelles, citons d'abord la prédominance du balaou japonais (*Cololabis saira*) en 1976, certaines fluctuations de l'abondance des groupes d'âge du lançon du Pacifique (*Ammodytes hexapterus*) et du hareng du Pacifique (*Clupea harengus*), un changement dans les espèces de sébaste (*Sebastes*) et l'apparition d'argentines batypélagiques (*Nansenia candida*) en 1978. Au cours d'un été donné, le lançon et les sébastes ont dominé en juillet, alors que le hareng et le balaou ont été plus abondants en août. Les variations d'âge et de taille des espèces de lançon, la composition des sébastes et la fréquence d'apparition des balaous et des argentines aux îles Triangle et Pine sont synchronisées au cours des ans. Le balaou compose une plus grande proportion du régime alimentaire des oiseaux qui se nourrissent dans les eaux de l'île Triangle et est remplacé par le hareng dans les îles côtières Pine et Lucy.

Les populations de poissons juvéniles qui habitent les eaux de surface sont très difficiles à étudier par les méthodes classiques d'échantillonnage de la zone pélagique. Les études du régime alimentaire de l'Alque à bec cornu, complétées par des études de capture au filet, permettent donc d'échantillonner les populations et d'analyser les classes d'âge des poissons juvéniles.

3. Introduction

The Rhinoceros Auklet (*Cerorhinca monocerata*) breeds from the Farallon Islands, California to the Sandman Reefs in Alaska in the northeastern Pacific and from the central east coast of Japan to northern Sakhalin and Kuril islands in the northern western Pacific (Udvardy 1963, Vermeer 1979). The birds nest in burrows about 1 m in length and lay one egg that hatches at the beginning of July. The chicks spend about 7 weeks in their burrows and leave the nesting island between mid August and mid September. During the nestling period each parent brings one meal of fish per night to the chicks (Richardson 1961). The diet of nestling Rhinoceros Auklets consists almost entirely of small fish (Vermeer 1979). The adults carry the fish crosswise in their bills which leaves the prey mostly intact and facilitates identification and measurement. It is during the chick-rearing period in July and August that prey can be adequately sampled, and changes in species and size determined. The effects of such changes on the growth and reproduction of Rhinoceros Auklet were reported in Vermeer and Cullen (1979) and Vermeer (1980).

The objective of this paper is to document the changes in fish species in meals brought by parent birds to their chicks, and the differences between inshore and offshore breeding localities in British Columbia. Ashmole and Ashmole (1968) suggested that tropical marine birds are indicators of relative prey availability. We also address the potential use of the fish diets of Rhinoceros Auklet nestlings as indicators of prey occurrence in temperate waters and as a method of studying age-classes of certain fish species that are extremely difficult to sample with conventional techniques.

4. Methods

Fish were collected from adult Rhinoceros Auklets in July and August on Triangle Island (50°52′N; 129°05′W), Pine Island (50°58′N; 127°41′W), and Lucy Island

(45°18'N; 130°37'W), British Columbia (Table 1). Triangle Island is exposed to the open North Pacific Ocean, whereas Pine and Lucy islands are sheltered by nearby land masses (Fig. 1). Triangle Island has no trees, whereas Pine and Lucy islands are covered with dense forests. These islands were selected because they contain the largest breeding colonies of Rhinoceros Auklets in British Columbia. We began food sampling on Triangle Island in July 1976, Pine Island was added in 1977, and Lucy Island in 1979. A major seasonal change in diet was observed the first week of August 1977 on Triangle Island, and all subsequent sampling included that time period. Sampling times were synchronized between islands whenever possible.

Rhinoceros Auklets were caught by hand with the aid of a bright flashlight directed on them as they landed with fish in their bills. Fish were placed in plastic bags and the birds released immediately. Collection sites were changed each night and the sampling time kept within 1 h to minimize disturbance to the birds. Sampling locations ranged from 50 to 400 m apart around the periphery of the islands. Localities with moderate slope angles and free of dense underbrush were selected to facilitate bird capture in the dark. Samples were placed in cold tap water and processed the same night (23:30–07:00). Whole fish were identified, weighed to the nearest 0.1 g with Pesola scales and their fork length (tip of snout to the fork of the tail) was measured to the nearest millimetre. About 5–10% of the prey brought to the chicks were damaged or consisted of unmeasurable pieces. These were weighed and identified when possible. Fish which could not be identified immediately, such as rockfish, were preserved in 5% formaldehyde solution. Rockfish were later identified in the laboratory.

A prey was defined as principal if it made up 10% or more of the bird's food biomass sampled in a given year, as common if less than 10% of the biomass, and as occasional if the prey occurred not more than six times during the study period at any island.

Statistical tests of significance between means were determined with two-tailed t-tests, and between proportions with Fisher-Exact tests. Common and scientific names follow Hart (1973).

5. Results

5.1. Prey composition and changes

The 2165 Rhinoceros Auklet meals collected on the three islands contained at least 10 000 fishes and weighed 65 kg (Table 1). The average bird meal was 30 g. Meal size increased significantly over the summer season in certain years (Table 1). At least 29 prey species were observed (Table 2). The principal foods included Pacific sandlance[1] at all three islands, Pacific herring on Pine and Lucy islands, and Pacific sauries on Triangle Island. In certain years other species gained importance. Rockfish were important in the birds' diet in 1978 and 1980. Bluethroat argentines were a major prey on Triangle Island in 1978, and to a lesser extent salmon were so on Pine Island in 1980.

Figure 1
Location of Pine, Lucy, and Triangle islands on the British Columbia coast

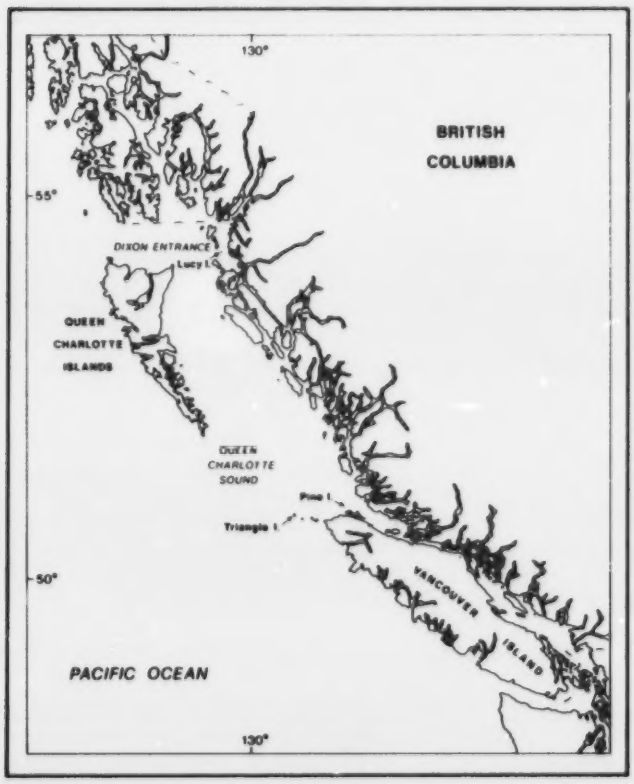


Table 1
Collection periods of food samples and meal sizes of Rhinoceros Auklets on Triangle, Pine, and Lucy islands, 1976–80

Location and year of sampling		Sampling periods	No. meals collected	Mean meal size and 95% confidence intervals, g	Meal range, g
Triangle Island	1976	16–25 July	14	34.6 ± 7.1	17.0–61.0
		1–15 August	16	38.8 ± 7.6	20.0–60.0
		16–31 August	17	35.8 ± 6.5	10.0–49.0
	1977	9–21 July	31	25.8 ± 5.7	9.0–48.5
		2–5 August	34	28.8 ± 4.9	9.0–59.0
		16–21 August	30	37.2 ± 5.2	13.0–51.0
	1978	4–12 July	36	25.0 ± 2.6*	4.0–47.0
		2–8 August	37	31.7 ± 2.7	16.0–51.0
		15–18 August	42	31.2 ± 3.0	11.5–52.0
	1979	1–6 July	55	21.0 ± 2.0*	10.5–42.4
		1–8 August	48	32.5 ± 2.9	14.9–57.4
		21–23 August	18	30.9 ± 4.8	7.1–49.8
Pine Island	1977	2–5 August	86	31.2 ± 3.2	9.4–68.0
	1978	5–11 July	152	29.4 ± 1.5*	8.0–56.0
		2–8 August	180	34.3 ± 1.4	13.0–63.0
		23–27 August	79	32.2 ± 1.8	16.0–61.0
	1979	1–6 July	111	28.5 ± 1.5	12.5–52.5
		1–8 August	186	28.6 ± 1.6	11.3–62.6
		17–20 August	128	27.6 ± 1.5	13.7–49.0
	1980	1–6 July	149	23.4 ± 1.6*	7.2–54.0
		1–5 August	152	32.6 ± 1.8	11.7–62.0
		18–21 August	133	32.8 ± 1.4	17.0–56.5
Lucy Island	1979	11–14 July	105	30.9 ± 1.8	12.4–61.1
		10–13 August	100	31.1 ± 2.0	13.0–55.7
	1980	10–13 July	99	29.0 ± 1.6*	14.2–53.3
		11–14 August	127	33.6 ± 1.8	14.5–63.5

*Mean significantly less than succeeding mean meal size ($P<0.05$).

[1] Table 2 gives scientific names of prey species.

Table 2
Prey species in Rhinoceros Auklet meals on Triangle, Pine, and Lucy islands, 1976–80 (P = principal, C = common, O = occasional; years in parentheses indicate predominance of particular prey species in those years only)

Prey species	Triangle 1976–79	Pine 1977–80	Lucy 1979–80
Pacific herring (*Clupea harengus*)	O	P	P
Northern anchovy (*Engraulis mordax*)	—	O	—
Chum salmon (*Oncorhynchus keta*)	O	C	C
Coho salmon (*Oncorhynchus kisutch*)	—	O	—
Sockeye salmon (*Onchorhynchus nerka*)	C	P (1980)	C
Whitebait smelt (*Allosmerus elongatus*)	—	O	—
Surf smelt (*Hypomesus pretiosus*)	—	—	O
Capelin (*Mallotus villosus*)	—	—	C
Eulachon (*Thaleichthys pacificus*)	O	O	—
Bluethroat argentine (*Nansenia candida*)	P (1978)	C (1978)	—
Slender barracudina (*Lestidium ringens*)	O	O	—
Blue lanternfish (*Tarletonbeania crenularis*)	O	—	—
Pacific cod (*Gadus macrocephalus*)	O	O	—
Walleye pollock (*Theragra chalcogramma*)	—	O	O
Pacific saury (*Cololabis saira*)	P	P (1977)	—
Pacific sandfish (*Trichodon trichodon*)	—	C	C
Pacific sandlance (*Ammodytes hexapterus*)	P	P	P
Pacific ocean perch (*Sebastes alutus*)	C (1979)	P (1979)	—
Dark-blotched rockfish (*Sebastes crameri*)	—	O	—
Widow rockfish (*Sebastes entomelas*)	P (1978)	P (1978,1980)	—
Yellowtail rockfish (*Sebastes flavides*)	P (1977)	P (1977)	—
Redstripe rockfish (*Sebastes proriger*)	—	O	—
Rockfish (*Sebastes* sp.)	—	—	O
Sablefish (*Anoplopoma fimbria*)	C	C	C
Kelp greenling (*Hexagrammos decagrammus*)	C	C	C
Ling cod (*Ophiodon elongatus*)	—	—	O
Cabezon (*Scorpaenichthys marmoratus*)	—	O	—
Flathead sole (*Hippoglassoides elassodon*)	—	O	—
Squid (*Loligo opalescens*)	C	C	C
Squid (*Berryteuthis anonychus*)	—	O	—

Sandlance, herring, and sauries made up 75% or more of the weight of bird meals. Sandlance accounted for 27, 31, and 59% of the food weights on Triangle, Pine, and Lucy islands, respectively (Table 3). Herring accounted for 43% on Pine Island and 33% on Lucy Island. Sauries made up 47% of the biomass on Triangle Island. These three species of prey, and rockfish, argentines, and salmon, together made up 95% or more of the total food biomass.

The incidence and weight of food species of Rhinoceros Auklet chicks varied among years (Table 3, Fig. 2). On Triangle Island, sandlance were scarce in 1976 but relatively abundant in later years. Sauries were the only prey of significance in 1976, but declined in importance as sandlance occurrence increased in other years. In 1978, however, both prey species were displaced by argentines in frequency of occurrence and percent biomass. On Pine Island, herring complemented sandlance in occurrence and biomass. In any given year, when sandlance were less important, herring were dominant in the birds' diet. The near doubling of herring biomass from 1977 to 1978 and from 1979 to 1980 relate to the predominance of first-year fish in 1977 and 1979 and second-year fish in 1978 and 1980. Similar complementary occurrences between sandlance and herring were observed on Lucy Island.

Rockfish occurred in the diet of Rhinoceros Auklet chicks on Triangle and Pine islands. They were high in occurrence but relatively low in biomass due to their small sizes. A distinct, remarkably similar yearly shift in rockfish species took place in both locations (Table 4). In 1977, the yellowtail rockfish was the sole species occurring at Triangle and Pine islands except for one occurrence of redstripe rockfish. In 1978, the widow rockfish was the sole rockfish species on both islands; in 1979, it was the Pacific ocean perch.

The incidence and weight of principal prey changed over the summer months (Table 5 and Fig. 3). Sandlance and rockfish occurred more frequently in the diet in July ($P<0.05$). Sauries and herring occurred more in August ($P<0.05$), except for 1976 when sauries predominated throughout the nesting period.

Table 3
Percentage occurrence (%O) and biomass (%B) of various fish in Rhinoceros Auklet meals

	Sandlance		Herring		Sauries		Rockfish		Argentines		Salmon		Other fish and squid
Year	%O	%B	%O	%B	%O	%B	%O	%B	%O	%B	%O	%B	%B
Triangle Island													
1976	6.4	3.7	2.1	1.8	95.7	90.7	—	—	—	—	4.3	2.4	1.4
1977	62.1	45.8	2.1	1.0	38.3	44.3	27.6	3.5	—	—	1.1	0.9	4.5
1978	11.3	7.4	0.9	0.4	23.8	22.7	33.0	15.5	78.3	48.6	0.9	1.0	4.4
1979	54.5	41.5	1.7	0.9	44.6	52.9	12.4	1.8	0.8	0.1	0.8	0.3	2.5
1976–79($\bar{x}$)	37.3	26.6	1.3	0.8	42.9	47.3	20.8	6.1	24.1	14.9	1.3	1.0	3.2
Pine Island													
1977	66.3	42.5	34.1	15.3	19.8	29.2	27.1	5.5	—	—	5.8	4.4	3.1
1978	31.4	28.0	45.7	48.0	5.4	4.3	16.5	8.9	5.6	4.5	5.4	4.8	1.5
1979	63.9	51.5	43.6	30.8	4.9	5.2	5.4	2.4	0.2	0.03	8.6	6.7	3.4
1980	22.1	12.0	51.4	56.3	1.1	1.1	25.6	12.7	—	—	15.9	13.1	4.8
1977–80($\bar{x}$)	40.9	30.9	46.3	43.3	4.8	5.2	16.5	7.9	1.8	1.5	9.8	7.9	3.3
Lucy Island													
1979	75.6	68.5	20.5	22.1	—	—	1.0	0.05	—	—	7.3	5.8	3.5
1980	59.3	50.2	46.5	42.8	—	—	—	—	—	—	5.3	2.8	4.2
1979–80($\bar{x}$)	65.9	58.9	34.1	32.9	—	—	0.5	0.02	—	—	6.3	4.2	4.0

5.2. Yearly changes in size of principal prey

The length of sandlance in Rhinoceros Auklet meals varied significantly among years (Table 6, Fig. 4). There are no data on the age of Pacific sandlance in British Columbia waters, so we assumed that those in the 40–110 mm length increment represent first-year fish and those in the 100–180 mm increment were second-year and older fish. This assumption agrees approximately with the age distribution of sandlance in Alaskan waters (Hatch, this volume; Dick and Warner, in press). First-year sandlance predominated on Triangle and Pine islands in 1977 and 1979, and on the latter in 1980. Second-year and older fish occurred most frequently on both islands in 1978. A bimodal distribution of sandlance lengths was observed on Lucy Island in 1979 and 1980, representing first-year and older age groups. Comparison of the overall length and biomass distribution of sandlance on Triangle, Pine, and Lucy islands indicate that first-year fish far outnumbered older ones, but the biomass of the latter was of about equal importance to the birds (Fig. 5).

Herring, like sandlance showed a distinct year-to-year difference in average length (Table 6) and in length distribution (Fig. 6). The 40–100 mm and the 100–180 mm length increments represent first- and second-year fish, respectively (Taylor *et al.* 1957). The bimodal distribution of

Table 4
Percentage occurrence (%O) and biomass (%B) of rockfish species in Rhinoceros Auklet meals on Triangle and Pine islands, 1977–80

	1977		1978		1979		1980	
Rockfish species	**%O**	**%B**	**%O**	**%B**	**%O**	**%B**	**%O**	**%B**
Triangle Island								
Yellowtail rockfish	27.6	3.5	—	—	—	—	—	—
Widow rockfish	—	—	33.0	15.5	—	—	—	—
Pacific ocean perch	—	—	—	—	12.4	1.8	—	—
Pine Island								
Yellowtail rockfish	25.9	5.4	—	—	—	—	—	—
Widow rockfish	—	—	16.5	8.9	—	—	25.1	12.4
Pacific ocean perch	—	—	—	—	5.4	2.4	—	—
Dark-blotched rockfish	—	—	—	—	—	—	1.4	0.3
Redstripe rockfish	1.2	0.07	—	—	—	—	—	—

Figure 2
Changes in food biomass of Rhinoceros Auklet nestlings among years

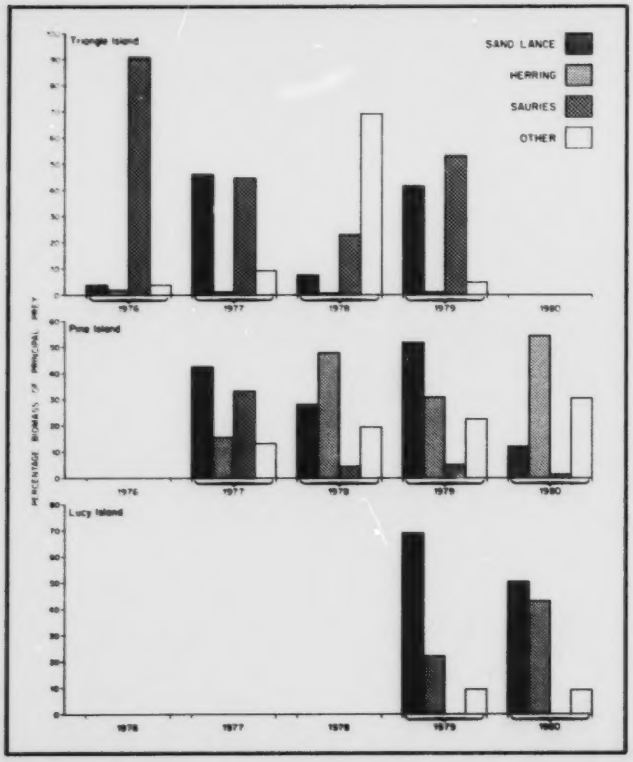
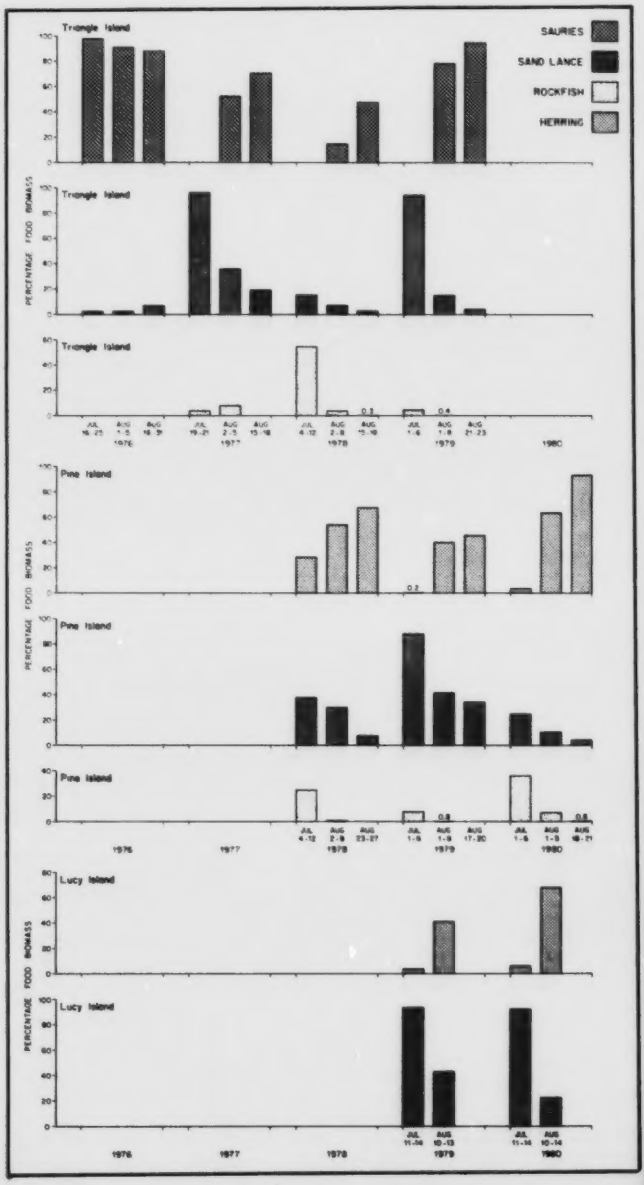


Figure 3
Changes in food biomass of Rhinoceros Auklet nestlings over the summer months



herring in 1978 and 1980 on Pine Island, and in 1980 on Lucy Island represent first- and second-year fish. The overall size distribution of herring on Pine and Lucy islands showed that first- and second-year age-classes are more distinct than those of sandlance (Figs. 4 and 6). As with sandlance first-year herring vastly outnumbered second-year fishes but the latter were much more substantial as a food source to the birds (Fig. 7).

Pacific sauries were the largest fish in the diet of nestling Rhinoceros Auklets (Table 6). The mean lengths of sauries collected at Triangle and Pine islands were not significantly different. Saury lengths in the diets on Triangle and Pine islands showed a 30–230 mm length range (Fig. 8). The 30–230 mm long sauries may all be first-year fish because Hughes (1974) reported two spawning periods per year (April–June and August–November) in this region.

Rockfish lengths were unimodal and represent only one age group of each species (Fig. 9). Differences between lengths of rockfish from Triangle and Pine islands were not significant (Table 6). All specimens were probably in their first year because they averaged much shorter than 1-year-olds (Phillips 1964, Westrheim and Harling 1975).

Bluethroat argentine lengths were unimodal and, like sandlance, rockfish, and sauries, of similar size on Triangle and Pine islands (Table 6 and Fig. 10). We found no information to establish the age of the argentines. Mean lengths of sockeye salmon were similar on Pine and Lucy islands (Table 6) and were most likely second-year fish (Foerster 1968).

Sizes of bluethroat argentines (Fig. 10) and first-year sandlance (Table 7) also varied over a given summer. Hatch (this volume) ascribed the increase in prey size in the

Figure 4
Length distribution of Pacific sandlance in Rhinoceros Auklet meals

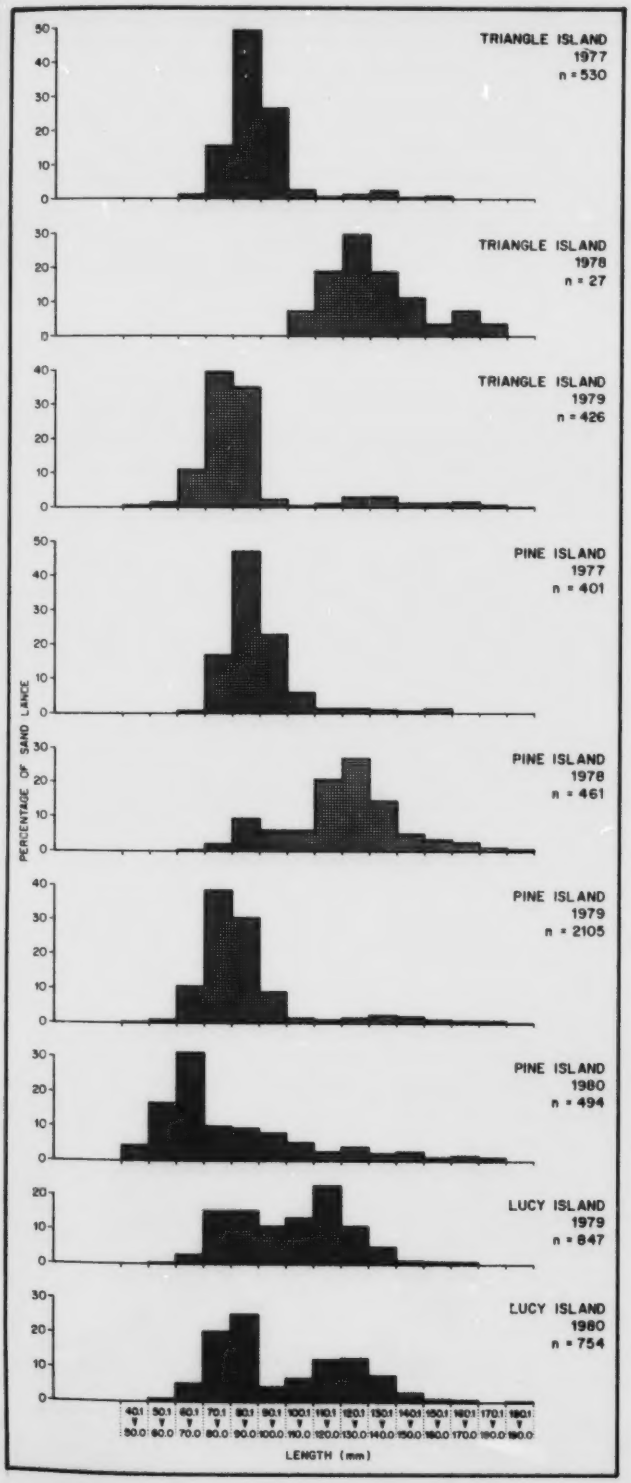
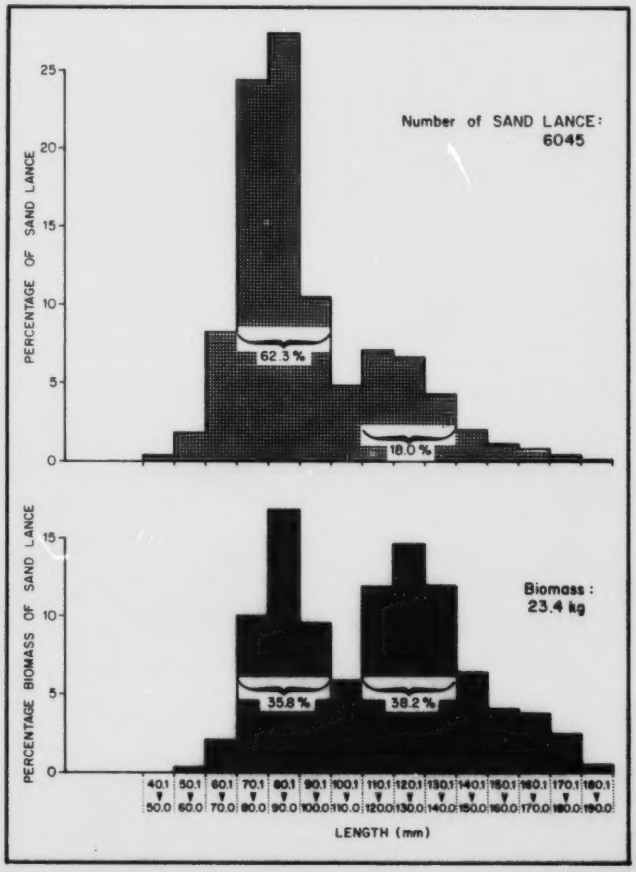

TRIANGLE ISLAND 1977 n = 530
TRIANGLE ISLAND 1978 n = 27
TRIANGLE ISLAND 1979 n = 426
PINE ISLAND 1977 n = 401
PINE ISLAND 1978 n = 461
PINE ISLAND 1979 n = 2105
PINE ISLAND 1980 n = 494
LUCY ISLAND 1979 n = 847
LUCY ISLAND 1980 n = 754
PERCENTAGE OF SAND LANCE
LENGTH (mm)

Figure 5
Overall frequency distribution of lengths and weights of Pacific sandlance in Rhinoceros Auklet meals



northern Gulf of Alaska during the summer months to growth. This cannot be ascertained from our data because auklets fed on fish of different year-classes over the summer which may or may not overlap in size (e.g. see Fig. 11), and the length of fish may vary among schools of the same year-class.

6. Discussion

6.1. Diet composition and prey occurrence

The composition of prey species in the food of nestling Rhinoceros Auklets may be influenced by the feeding location (offshore *vs.* inshore and northern *vs.* southern waters), random availability in the marine environment, timing of prey occurrence, and water temperatures.

The predominance of certain fish species in bird meals reflects their occurrence near auklet colonies. On the basis of observations by Cody (1973) and Wahl *et al.* (1979), more than 30% of the Rhinoceros Auklet breeding population should feed within 50–60 km of their respective islands. Sandlance are common prey for many commercial fish species and several fish-eating birds from Alaska to Washington (Hart 1973, Harris and Hartt 1977, Ainley and Sanger 1979, Vermeer 1979). In summer they are numerous inshore at depths of less than 50 m (Harris and Hartt 1977). Herring are numerous inshore during their first summer (Hourston 1958, 1959) and are important for many inshore subarctic birds (Ainley and Sanger 1979). The Pacific saury is an abundant warm-water and offshore species (Inoue and Hughes 1971) and is important as prey of Sooty Shearwaters (*Puffinus griseus*) (Chu, this volume; Ogi, this volume). The predominance of sauries in the auklet diet only at offshore Triangle Island, and that of herring only at inshore Pine and Lucy islands suggest differences in available prey species in offshore and inshore waters.

Figure 6
Length distribution of Pacific herring in Rhinoceros Auklet meals

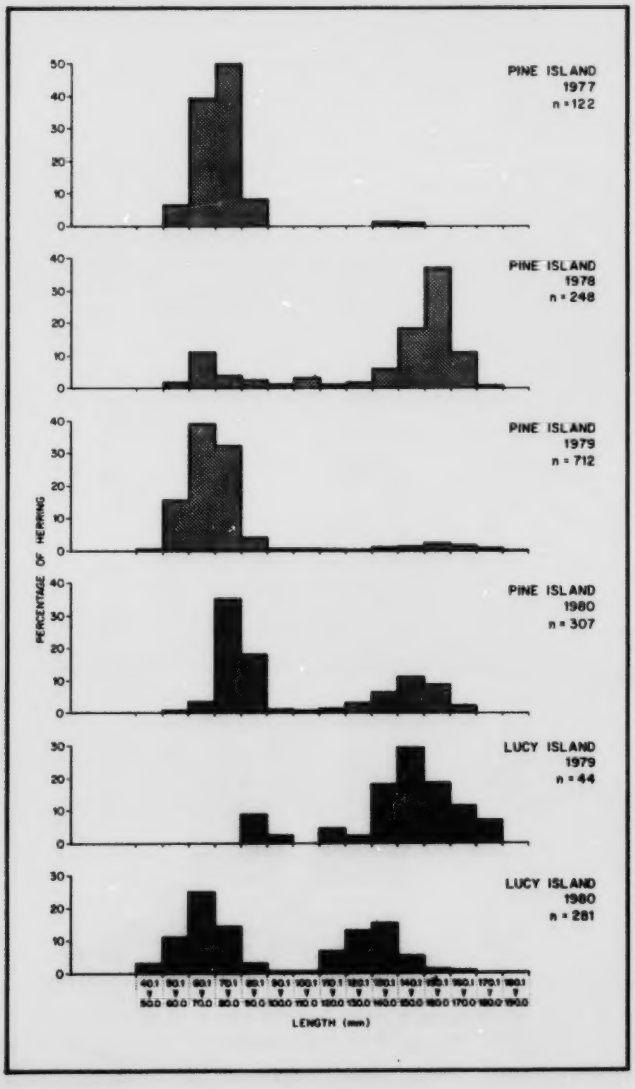
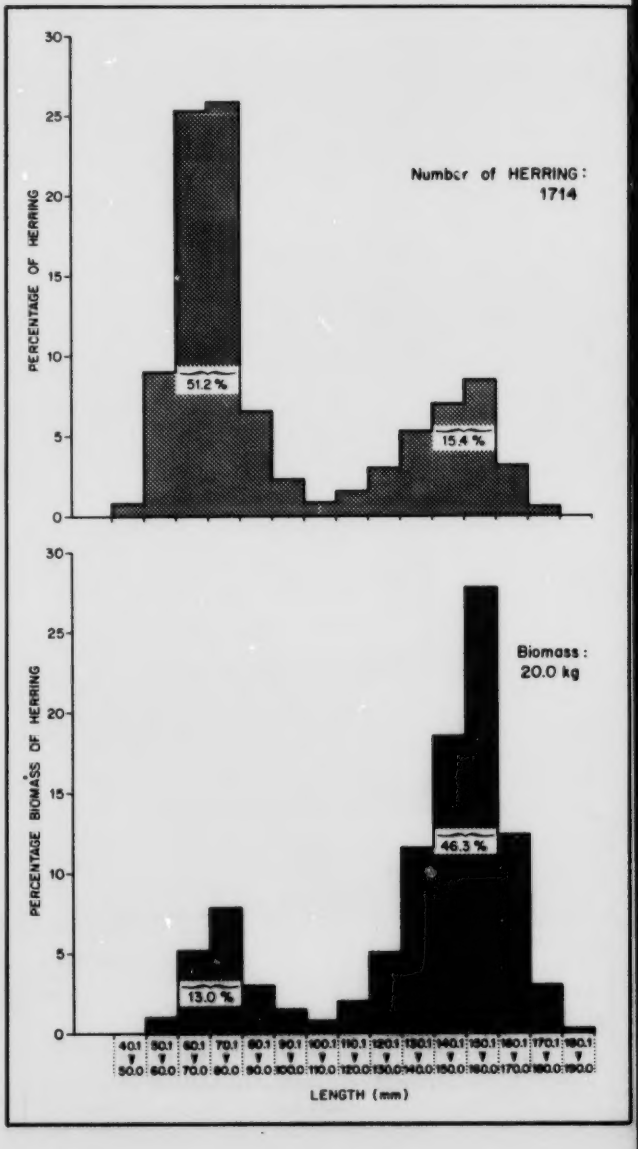


Figure 7
Overall frequency distribution of lengths and weights of Pacific herring in Rhinoceros Auklet meals



The common appearance of capelin as bird food at Lucy Island and their absence at Triangle and Pine islands suggests availability of capelin in northern British Columbia waters. Capelin is one of the most numerous fish and constitutes the main prey of many fish in Alaska (Harris and Hartt 1977). It is an important food for several fish-eating bird species in the northern North Pacific and Bering Sea but not farther south (Ainley and Sanger 1979; Vermeer 1979; Krasnow and Sanger, in press; Sanger, in press). Rockfish were principal prey of Rhinoceros Auklets in more southern waters of Triangle and Pine islands, and an occasional prey at northern Lucy Island. Rockfish are uncommon in the diet of fish-eating birds in northern areas (Ainley and Sanger 1979).

Bluethroat argentines, a cold water, bathypelagic species (Hart 1973) suddenly occurred in Rhinoceros Auklet food almost exclusively in 1978 (except for one fish in 1979). It was also a major prey of chinook (*Oncorhynchus tshawytscha*) and sockeye salmon along the northwest coast of Vancouver Island in 1978, an unusual phenomenon not previously recorded (A. Ostrom, pers. comm.). The occurrence of argentines in salmon stomachs that year supports the view that a species abundant in the birds' diet may also be abundant in the marine waters.

The timing of prey occurrence is critical to its appearance in the bird diet. Sockeye and pink salmon (*O. gorbuscha*) are abundant in Hecate Strait and Queen Charlotte Sound (Aro *et al.* 1977). Sockeye salmon are common prey of Rhinoceros Auklets in July and August but pink salmon are not. The migration of pink salmon from those waters to the North Pacific Ocean in May and June (LeBrasseur and Parker 1964) explains their absence in the diet of nestling Rhinoceros Auklets.

Sauries are warm-water fish and their increase in the Rhinoceros Auklet diet in August (except in 1976) may be explained by the increasing surface water temperatures, which on the average increase at least 1°C per month from June to August in British Columbia waters (Dodimead 1980, Vermeer 1980). It is unknown why sauries predominated in auklet meals before August in 1976 at Triangle Island, because nearshore surface water temperatures then were generally lower than in August of succeeding years (Vermeer 1980). The changes in occurrence of herring and rockfish over the summer are not understood. Rockfish may be affected by surface water temperatures like the sandlance which move into deeper water in late summer and fall (Andriyashev 1954). Herring appear simultaneously with sauries in late summer, and may be positively influenced by the higher surface water temperatures at that time.

6.2. Changes in prey size

The repetitive seasonal changes in diet composition, age classes of prey, and in appearance of argentines and species of rockfish in the diet at both Triangle and Pine islands over several years indicate that Rhinoceros Auklets fed upon fish of the same age group and species each year but they differed between years. Along with the auklets, Tufted Puffins (*Fratercula cirrhata*) on Triangle Island fed on the same age groups of sandlance and the same species of rockfish each year, and on bluethroat argentines in 1978 (Table 8). All these observations support the hypothesis that the diet of nestling Rhinoceros Auklets reflects changes in availability of juvenile fish in coastal waters.

Table 5
Occurrence (%) of principal prey in Rhinoceros Auklet meals (see Table 1 for sample size). Statistically significant changes are shown by pairs of letters (Stat. test: $P<0.05$)

	Triangle Island			Pine Island				Lucy Island	
Collection date	**Sandlance**	**Saury**	**Rockfish**	**Sandlance**	**Saury**	**Rockfish**	**Herring**	**Sandlance**	**Herring**
1976									
16–25 July	—	100	—	—	—	—	—	—	—
1–5 August	—	94	—	—	—	—	—	—	—
16–31 August	—	94	—	—	—	—	—	—	—
1977									
9–21 July	100[a]	0[c]	35	—	—	—	—	—	—
2–5 August	50[a]	44[c]	44[f]	66	19	27	34	—	—
16–21 August	37	70	0[f]	—	—	—	—	—	—
1978									
4–12 July	19	0[d]	86[g]	40	0	40[m]	24[p]	—	—
1–8 August	11	19[d]	14[g]	32[i]	2[l]	4[m]	55[p]	—	—
15–18 August	5	8	5[g]	—	—	—	—	—	—
23–27 August	—	—	—	13[i]	24[l]	0	66	—	—
1979									
1–6 July	100[b]	0[e]	25[h]	95[j]	0	18[n]	4[q]	—	—
11–14 July	—	—	—	—	—	—	—	97[s]	3[u]
1–8 August	21[b]	77[e]	2[h]	57[j]	4	2[n]	58[q]	—	—
10–13 August	—	—	—	—	—	—	—	53[s]	39[u]
17–20 August	—	—	—	49	11	0	59	—	—
21–23 August	6[b]	94	0	—	—	—	—	—	—
1980									
1–6 July	—	—	—	40[k]	0	53[o]	4[r]	—	—
11–14 July	—	—	—	—	—	—	—	97[t]	8[v]
1–5 August	—	—	—	16[k]	3	20[o]	62[r]	—	—
10–14 August	—	—	—	—	—	—	—	30[t]	76[v]
18–21 August	—	—	—	8	1	2[o]	93	—	—

6.3. Rhinoceros Auklets as sampling devices

Juvenile fish populations in surface waters are very difficult and extremely expensive to study by conventional sampling methods. The distribution of juvenile fish populations is highly patchy and sample variability with nets is so great that even species composition can be barely touched. Determination of density distributions even for small areas are very costly. The bird's diet provides a means of sampling juvenile fish populations and could prove to be useful in monitoring age-classes of certain fish species. We recognize the need for complementary sampling with nets to establish the relationships of juvenile fish in marine waters to those observed in the diets of nestling Rhinoceros Auklets. Joint efforts between fisheries and seabird biologists would enhance our understanding of the distribution and structure of juvenile fish populations and their availability to marine birds. Neither discipline in itself can provide an understanding of the changes that occur in these juvenile populations and their implications for the marine-bird food chain.

Table 6
Length of principal prey in Rhinoceros Auklet meals on Triangle, Pine, and Lucy islands, 1976–80

Species and location	Year	No. of fishes	Average length and 95% conf. int., mm
Pacific sandlance			
Triangle	1976	14	122.6 ± 14.6
	1977	530	88.6 ± 1.0
	1978	27	131.7 ± 9.5
	1979	426	84.5 ± 2.0
Pine	1977	401	89.7 ± 1.4
	1978	461	120.4 ± 2.7
	1979	2105	84.9 ± 0.9
	1980	494	79.4 ± 2.6
Lucy	1979	847	102.2 ± 1.5
	1980	754	98.8 ± 1.8
Herring			
Pine	1977	122	71.7 ± 1.9
	1978	248	133.1 ± 4.3
	1979	708	74.4 ± 1.8
	1980	307	99.8 ± 3.5
Lucy	1979	44	141.1 ± 7.0
	1980	277	95.1 ± 4.0
Pacific saury			
Triangle	1976	75	179.1 ± 6.2
	1977	59	173.8 ± 8.0
	1978	43	179.1 ± 5.8
	1979	89	144.1 ± 5.2
Pine	1977	31	179.2 ± 5.8
	1978	49	140.9 ± 7.0
	1979	37	151.8 ± 8.7
Yellowtail rockfish			
Triangle	1977	64	52.7 ± 1.3
Pine	1977	92	55.0 ± 1.5
Widow rockfish			
Triangle	1978	160	66.8 ± 1.0
Pine	1978	302	66.6 ± 0.8
	1980	514	61.2 ± 0.7
Pacific ocean perch			
Triangle	1979	19	61.6 ± 3.0
Pine	1979	73	63.1 ± 1.5
Bluethroat argentine			
Triangle	1978	279	100.0 ± 1.2
Pine	1978	103	102.6 ± 1.6
Sockeye salmon			
Pine	1977–80	95	124.8 ± 2.9
Lucy	1979–80	21	122.8 ± 8.4

Table 7
Comparison of length of Pacific sandlance brought by Rhinoceros Auklets to their chicks on Triangle and Pine islands, 1977 and 1978

Sample location	Time of sampling	No. of fishes	Mean length and 95% conf. int., mm
Triangle Island	July 1977	369	85.5* ± 0.9
	August 1977	161	95.1 ± 2.5
Pine Island	July 1978	209	120.5 ± 2.7
	August 1978	252	120.3 ± 2.7

*Statistically significant from succeeding mean ($P<0.05$).

Figure 8
Length distribution of Pacific sauries in Rhinoceros Auklet meals

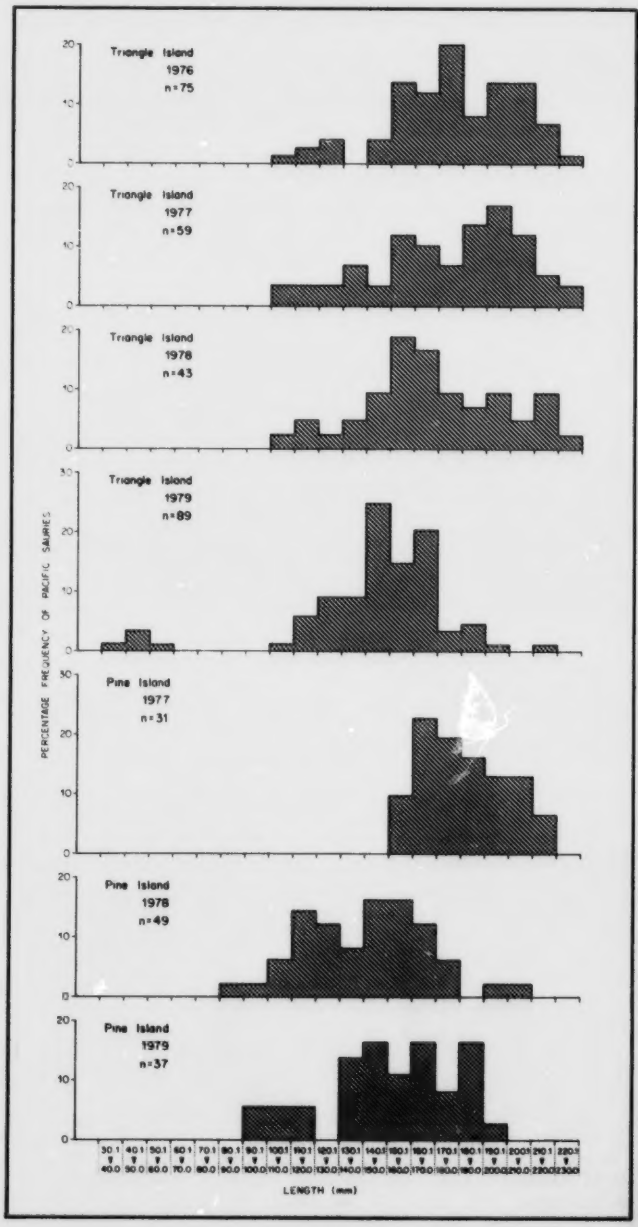


Figure 9
Length distribution of rockfish in Rhinoceros Auklet meals

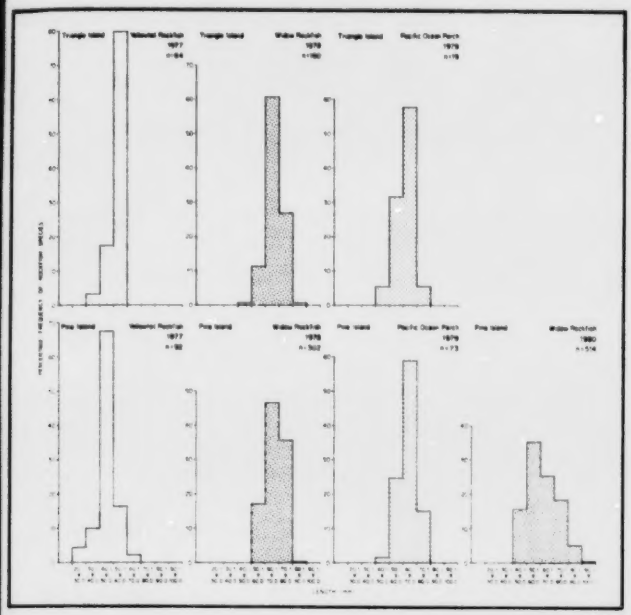


Figure 10
Length distribution of bluethroat argentines in Rhinoceros Auklet meals, Pine and Triangle islands, 1978

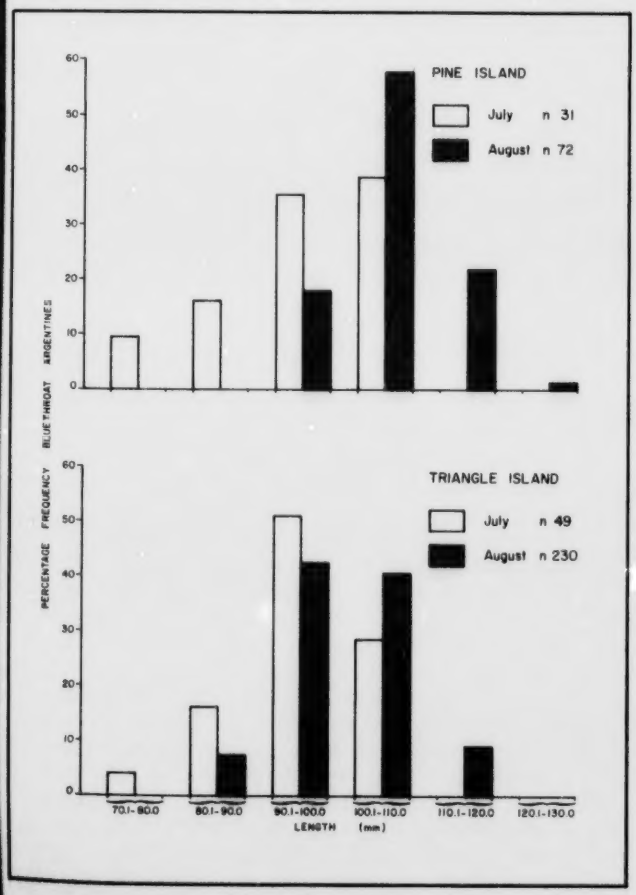


Figure 11
Length distribution of Pacific herring in Rhinoceros Auklet meals on Pine Island for different periods in 1978

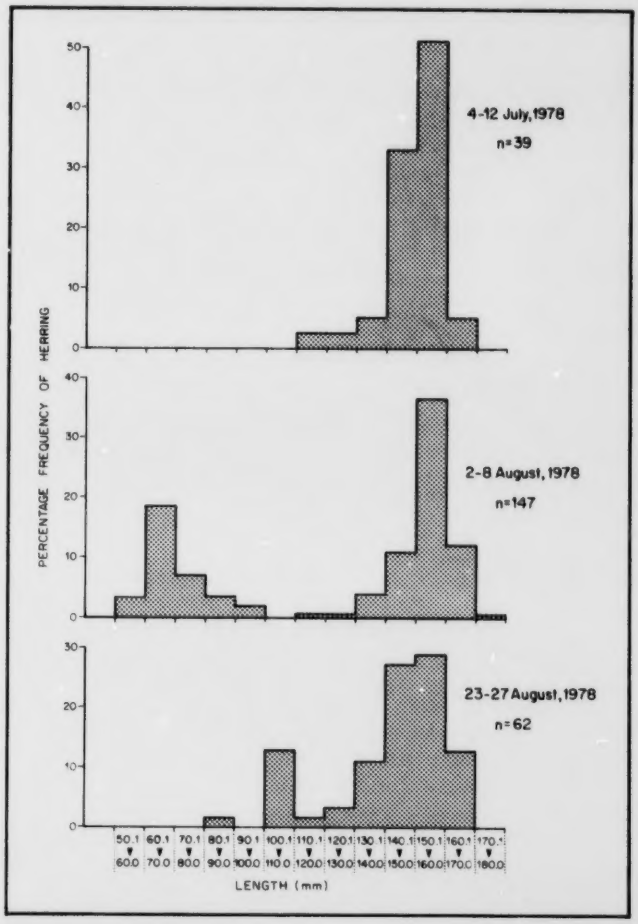


Table 8
Comparison of lengths of Pacific sandlance, yellowtail and widow rockfish, and bluethroat argentines brought by Rhinoceros Auklets and Tufted Puffins to their chicks on Triangle Island in July and August 1977 and 1978

Bird species, year	Fish species	No. of fish	Mean length and 95% conf. int., mm
Rhinoceros Auklet, 1977	Pacific sandlance	530	88.6 ± 1.0*
Tufted Puffin, 1977	Pacific sandlance	80	84.9 ± 5.8
Rhinoceros Auklet, 1978	Pacific sandlance	27	131.7 ± 9.5
Tufted Puffin, 1978	Pacific sandlance	35	125.0 ± 5.2
Rhinoceros Auklet, 1977	yellowtail rockfish	64	52.7 ± 1.3
Tufted Puffin, 1977	yellowtail rockfish	14	54.3 ± 2.8
Rhinoceros Auklet, 1978	widow rockfish	160	66.8 ± 1.0
Tufted Puffin, 1978	widow rockfish	16	67.2 ± 3.1
Rhinoceros Auklet, 1978	bluethroat argentine	279	100.0 ± 1.2
Tufted Puffin, 1978	bluethroat argentine	47	100.0 ± 6.9

*Vermeer (1980) reported significantly longer Pacific sandlance in Rhinoceros Auklets than in Tufted Puffins for smaller August samples only, which included second-year fish for Rhinoceros Auklets, but not for puffins.

7. Acknowledgements

We thank Captain W.M. Exley and E. Harris of the Canadian Coast Guard for accommodation and lightkeepers A. Babitz, K. Nuttall, C. Plumpton, and G. Watson and their families for their generous hospitality extended to the senior author and his daughter, Lotus, at the light stations on Pine and Lucy islands. Lotus assisted with field work. We are much obliged to J.B. Foster for permission to work on the ecological reserve of Triangle Island and to L. Cullen, R. Billings, and K. Summers for assistance with field work. W.R. Harling and A. Peden helped identify prey items and D. Ainley, G.A. Sanger, R.A. Vermeer, and two anonymous referees reviewed an earlier draft of the manuscript and made pertinent comments. This study was financially supported by the Canadian Wildlife Service.

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Nestling diet and feeding rates of Rhinoceros Auklets in Alaska

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1. Abstract

Food brought to nestling Rhinoceros Auklets (*Cerorhinca monocerata*) was sampled by applying tape or cloth muzzles to the chicks and collecting the uningested food from the burrow daily. Limited data were also gathered for Tufted and Horned puffins (*Fratercula cirrhata* and *F. corniculata*). Auklet chicks received an average of 34.1 g of food per night at Middleton Island in 1978, and 32.8 g per night at the Semidi Islands in 1979. Pacific sandlance (*Ammodytes hexapterus*) made up the bulk of the diet at both locations, and large, second-year or older fish predominated in the samples. In contrast, Horned and Tufted puffins took mostly small, first-year fish during the same seasons. The quantity of food delivered per night to Rhinoceros Auklets increased with the age of the chick, and wind speed may have been an important environmental factor affecting feeding rates. Proportions of first-year and older sandlance in the diet varied within and between sampling bouts, indicating spatial and temporal changes in prey availability. Parallel changes in feeding rates were also observed. The primary use of different age groups of sandlance by the three puffin species suggests the age structure of the prey population may differentially affect breeding success.

2. Résumé

Nous avons échantillonné la nourriture apportée à de jeunes Alques à bec cornu (*Cerorhinca monocerata*) par l'application de muselières faites de ruban adhésif ou de tissu aux oisillons et par la collecte quotidienne des aliments non ingérés se trouvant dans le terrier. Nous avons également réuni un certain nombre de données pour les Macareux huppés et les Macareux cornus (*Fratercula cirrhata* et *F. corniculata*). Les jeunes alques ont reçu en moyenne 34,1 g de nourriture par nuit à l'île Middleton en 1978, et 32,8 g par nuit aux îles Semidi en 1979. Le lançon du Pacifique (*Ammodytes hexapterus*) compose le gros du régime alimentaire aux deux endroits et les gros poissons âgés de deux ans ou plus dominent dans les échantillons. En revanche, les Macareux huppés et les Macareux cornus ont généralement capturé de petits poissons d'un an au cours des mêmes années. La quantité de nourriture livrée chaque nuit aux jeunes alques augmente en fonction de l'âge du juvénile. La vélocité du vent peut avoir été un facteur environnemental important influant sur les taux d'alimentation. Les proportions de lançons âgés d'un an et plus dans le régime varient d'une période d'échantillonnage à l'autre et dans une même période, ce qui témoigne des variations spatio-temporelles de la disponibilité des proies. Nous observons également une évolution parallèle des taux d'alimentation. Les principales utilisations des divers groupes d'âge de lançon par les trois espèces de macareux donnent à penser que la structure d'âge des proies peut différemment influer sur la réussite de la reproduction.

3. Introduction

Recent studies on the breeding biology of puffins have generated considerable information on foods and feeding ecology during the chick period. The Atlantic Puffin (*Fratercula arctica*) is especially well known in this respect (Pearson 1968, Nettleship 1972, Corkhill 1973, Harris 1978, Hudson 1979, Ashcroft 1979), whereas three North Pacific species, including the Rhinoceros Auklet (*Cerorhinca monocerata*) (Storer 1945), have received comparatively little attention. Information is available for Rhinoceros Auklets and Tufted Puffins (*Fratercula cirrhata*) at colonies in Washington (Cody 1973, Leschner 1976, Wilson 1977) and British Columbia (Vermeer 1979; Vermeer *et al.* 1979; Vermeer and Westrheim, this volume; Summers and Drent 1979). Information for Alaska, where large numbers of all three species breed, has only recently become available (Amaral 1977, Wehle 1980).

Results of investigations on puffins support three general conclusions: (1) the food delivered to chicks usually includes very few species of prey at any one place and time; (2) nestling diets commonly exhibit annual, geographic, and seasonal variation, which presumably reflects changes in the availability of potential prey; (3) such variation affects chick growth and survival, and therefore reproductive success.

This paper is based on food samples collected in 1978 and 1979 at two colonies of the Rhinoceros Auklet in Alaska. The main objectives are (1) to examine variation in the nestling diet of this species, along with supplemental information for the Tufted Puffin and Horned Puffin (*Fratercula corniculata*); (2) to identify factors that affect feeding rates in the Rhinoceros Auklet; and (3) to suggest some possible effects of prey population structure on the breeding ecology of puffins.

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4. Study areas

The two study sites are about 700 km apart in the central and western Gulf of Alaska. Middleton Island lies in the path of the Alaska Current (Favorite *et al.* 1976), 90 km from the Alaska mainland and 20 km from the edge of the continental shelf (Fig. 1). The island measures about 1.5 by 8 km and is used by seven species of breeding seabirds totalling around 175 000 individuals. In 1978, Rhinoceros Auklets occurred in four well isolated subcolonies totalling some 1800 birds. An estimated 3000–5000 Tufted Puffins nested at low density around much of the perimeter of the island. Food samples of both species were collected at several points around the island. No Horned Puffins breed on Middleton Island.

The Semidi Islands include nine islands and numerous smaller islets and rocks 80 km south of the Alaska Peninsula near longitude 156° W. The edge of the continental shelf lies some 80 km to the south. Collectively, these islands support the largest breeding aggregation of marine birds in the Gulf of Alaska (2.4 million birds of 20 species), although Rhinoceros Auklets are relatively uncommon (Sowls *et al.* 1978). They are known to breed only on Chowiet Island where they number about 800 birds. Tufted Puffins (100 000) and Horned Puffins (375 000) nest on all islands in the group. Food samples of these species were collected primarily at Kateekuk Island, 2 km to the northwest of Chowiet, and at Suklik Island, 3 km to the east.

5. Methods

5.1. Field technique

Food samples were obtained primarily by applying a muzzle to the chick to prevent it from swallowing any of the food delivered by its parents, and collecting the accumulated food from the floor of the nest chamber daily. At Middleton Island, fibre-reinforced packaging tape was folded and tied in a harness around the bill and back of the head (Baird and Moe 1978). Boot-shaped cloth hoods were used to cover the entire head at the Semidi Islands. Three sizes were sewn to fit chicks of various ages. A draw string of yarn around the lower margin, tied at the nape, prevented the hood from slipping off. Hoods were preferable to tape because they caused less stress and, unlike tape, were never removed by the chicks. The procedure was also more efficient because hoods were reusable and simpler to apply. I refer to food samples collected by this method as "burrow-loads"; samples collected directly from adults (e.g. Nettleship 1972, Corkhill 1973) I call "bill-loads."

Collections were made in four sampling periods 6–7 days apart at Middleton Island (18 July – 16 August 1978), and in three sampling periods 10–13 days apart at the Semidi Islands (18 July – 11 August 1979). A sampling period comprised two successive nights, i.e. each chick wore a muzzle for 36–48 h, but samples were collected each morning. Because Rhinoceros Auklets visited their nests only at night, each sample represents the quantity of food delivered to a chick in a 24-h period. Chicks were weighed at the outset of each sampling period and after each interval of fasting. Their ages were estimated from wing measurements on the first visit with reference to data for known-age chicks (Leschner 1976).

The method I have described had only limited success with Tufted and Horned puffins. Samples obtained from these species were supplemented with bill-loads or specimens of prey found on the ground near burrow entrances, but the total of material available for comparison with the auklets is minimal.

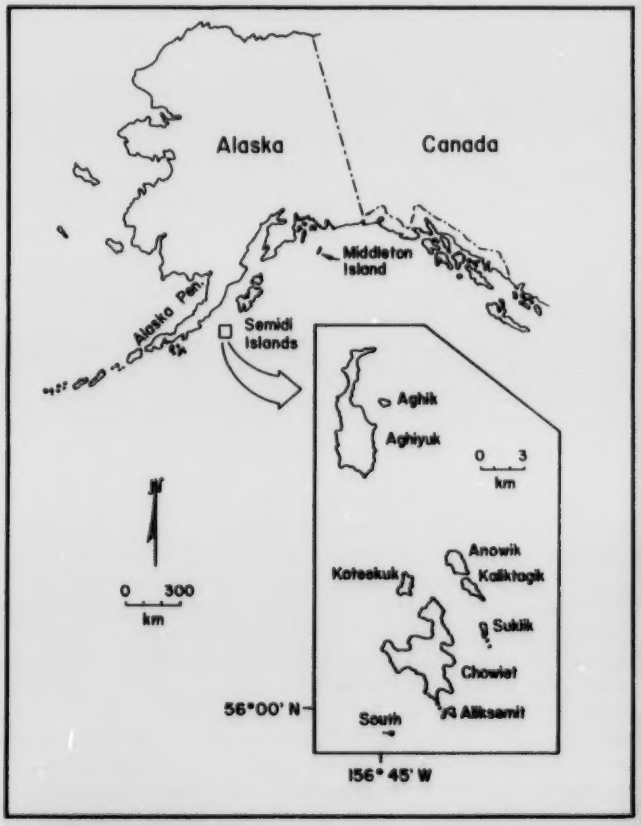
5.2. Laboratory technique

Food samples were preserved in 10% Formalin for later sorting and identification of species in the laboratory. Except as noted below, identifications were made by the author. Fish lengths were measured to the nearest millimetre from the snout to the tip of the tail. Age-classes of sandlance (*Ammodytes hexapterus*) were assigned by inspection of the distribution of lengths in my sample and distributions for known-age fish (Blackburn 1979; Dick and Warner, in press). Preserved burrow-loads were air dried for 2–3 min and weighed with a triple beam balance accurate to 0.1 g.

5.3. Statistical analysis

Most of the statistical analysis was accomplished using the SPSS package of computer programs (Nie *et al.* 1975). I used the arcsine transformation on percentages and an additional transformation ($Y \rightarrow Y^2$) on two variables (proportion of sandlance per burrow-load and relative proportion of second-year or older sandlance) to yield distributions with nonsignificant skewness and kurtosis.

Figure 1
Location of study sites in the Gulf of Alaska



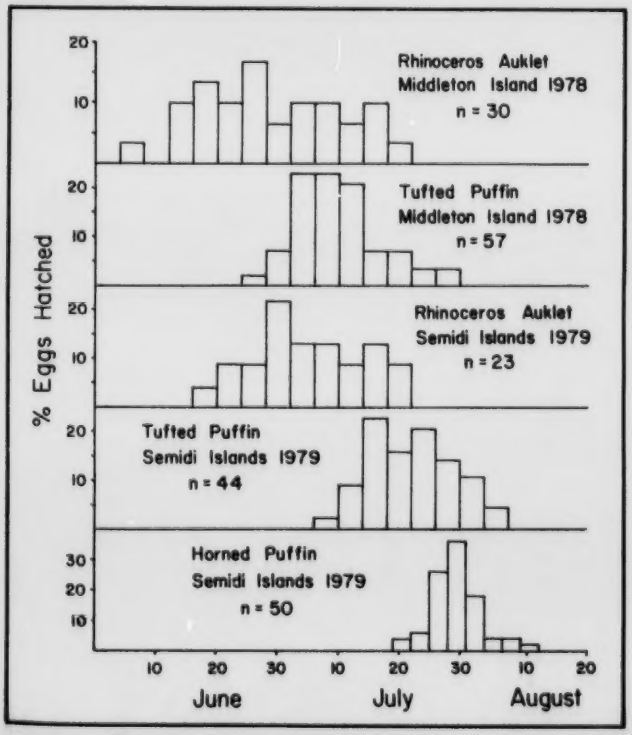
6. Results

6.1. Breeding phenology

Since the food available to seabirds varies seasonally and annually, it is useful to note differences in the timing of breeding among the three puffins. Rhinoceros Auklets probably breed earliest wherever these species occur together (Fig. 2; see also Vermeer *et al.* 1979). At Middleton Island their eggs hatched about 2 weeks earlier than those of Tufted Puffins, and at the Semidi Islands, about 3 weeks earlier. Horned Puffins, in turn, hatched 1 week later than Tufted Puffins at the Semidis. Breeding schedules were earlier at Middleton Island in 1978 than at the Semidis in 1979, about 1 week for Rhinoceros Auklets and 2 weeks for Tufted Puffins.

The fledging periods of Rhinoceros Auklets, Tufted Puffins, and Horned Puffins average 51, 47, and 40 days, respectively (Vermeer and Cullen 1979, Wehle 1980). The mean age of Rhinoceros Auklet nestlings from which food samples were collected was 33.1 days at Middleton Island (n = 68, SD = 11.0, range 3–54 days) and 28.1 days at the Semidis (n = 82, SD = 10.7, range 13–52 days). Tufted Puffins averaged 24.4 days old in the sample on Middleton Island (n = 16, SD = 8.1, range 10–33 days). Since only bill-loads were obtained from Tufted and Horned puffins at the Semidis, the ages of chicks in the sample can only be approximated from sampling dates and the distribution of hatching (Fig. 2). The mean age of Tufted Puffins would have been in the range 30–35 days; the mean for Horned Puffins was probably 20–25 days.

Figure 2
Hatching dates of puffins at Middleton Island in 1978 and the Semidi Islands in 1979



6.2. Feeding rates

The distribution of burrow-load-size for Rhinoceros Auklets did not differ significantly from the normal distribution at either study area (Kolmogorov-Smirnov test for goodness-of-fit, $P > 0.05$). Means and ranges of load-sizes were similar at the two sites (Table 1). Body weight, averaged over all sampling periods, was 270 g per chick at Middleton Island and 225 g per chick at the Semidi Islands. Thus, the rates of food intake can be expressed as 12.6% and 14.6% of body weight per day at the two sites, respectively. Muzzled chicks lost weight at an average rate of 8.6% of body weight per day.

The feeding of Tufted Puffins was severely disrupted by the same collecting technique that appeared to work well with Rhinoceros Auklets (Table 1, Appendix). No food was delivered to Tufted Puffins on over two-thirds of days compared with 16% and 11% of days, respectively, for Rhinoceros Auklets at Middleton Island and the Semidis.

6.3. Nestling diets

Rhinoceros Auklet nestlings at Middleton Island were fed almost entirely Pacific sandlance, plus small quantities of four other species of fish as well as squid and octopus (Fig. 3, Table 2). Sandlance also made up the bulk of the diet at the Semidi Islands (Fig. 4), but capelin (*Mallotus villosus*) made up 29% by weight in mid July, declining thereafter (Fig. 5). Capelin were lacking at Middleton Island, and there were no notable changes in the composition of the diet during the season. Although data for Tufted and Horned puffins are limited, they suggest marked differences between the diets of these species and that of Rhinoceros Auklets (Figs. 3 and 4). Tufted Puffins, in particular, had important prey other than sandlance, including cephalopods at Middleton Island and walleye pollock (*Theragra chalcogramma*) at the Semidis. Larval flatfish (mean length 35 mm) and a euphausiid, *Thysanoessa spinifera* (mean length 30 mm), occurred in several samples at the Semidis. Although these items were not quantitatively important, it is notable that such tiny prey were brought to

Table 1
Performance of the food sampling scheme at Middleton Island in 1978 and the Semidi Islands in 1979

	Middleton Island		Semidi Islands
Variable	Rhinoceros Auklet	Tufted Puffin	Rhinoceros Auklet
Effort, chick-days	101	68	95
No. days chick died or disappeared	11 (10.9%)	8 (11.8%)	0
No. days chick removed muzzle	9 (8.9%)	11 (16.2%)	3 (3.2%)
No. days no food delivered*	13 (16.0%)	33 (67.3%)	10 (10.9%)
No. loads collected	68	16	82
Weight per load, g			
mean†	39.6	13.4	36.4
SD	16.5	15.2	17.8
range	9.9–81.3	3.7–57.8	6.5–80.5
Overall feeding rate, g/day‡	34.1	—	32.8

*Percentages calculated after excluding instances in which the technique failed because the chick was lost or removed its muzzle.
†Mean for all sampling periods combined.
‡Rates include nights on which no food was delivered.

chicks. Similarly, one bill-load of a Horned Puffin consisted of 50 larval Osmerids, probably capelin, weighing less than 4 g in all.

Figure 3
Nestling diets of Rhinoceros Auklets and Tufted Puffins at Middleton Island, 26 July – 16 August 1978. Sample sizes are the number of burrow-loads

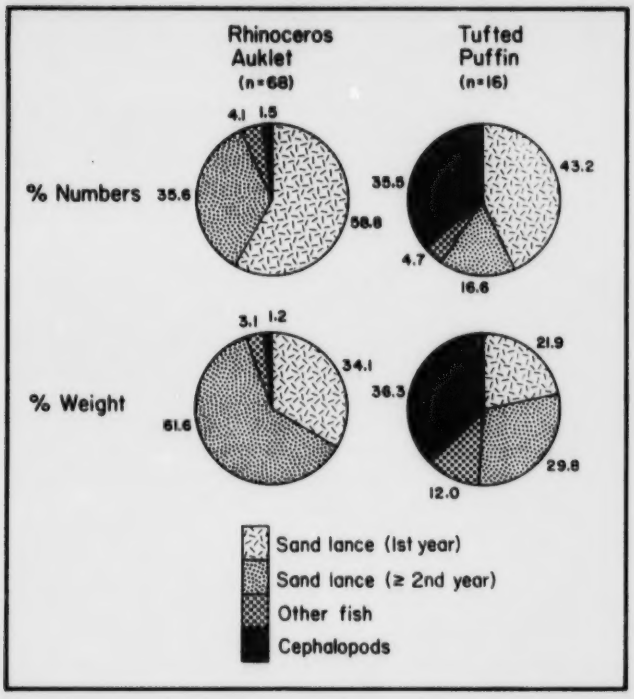


Figure 5
Temporal changes in the diet of Rhinoceros Auklets at the Semidi Islands in 1979. Samples are the number of burrow-loads

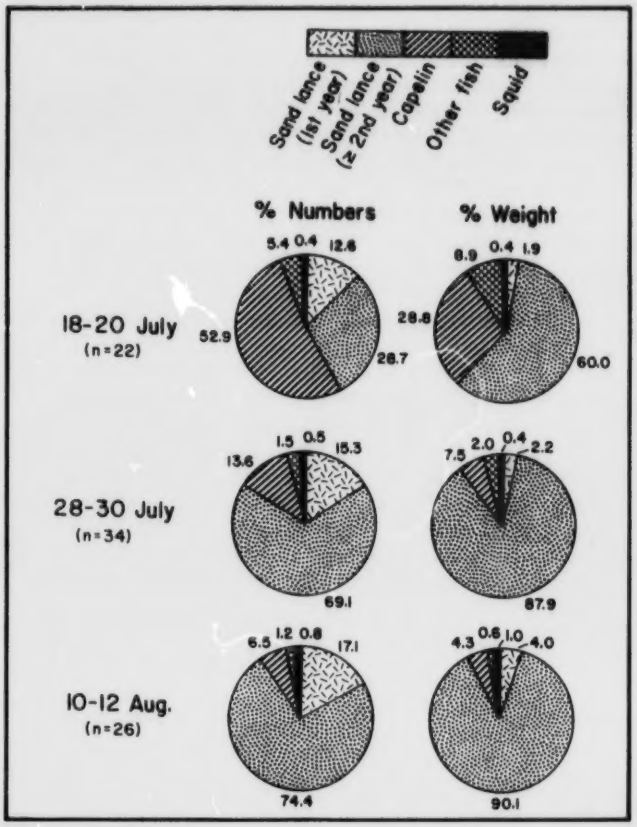
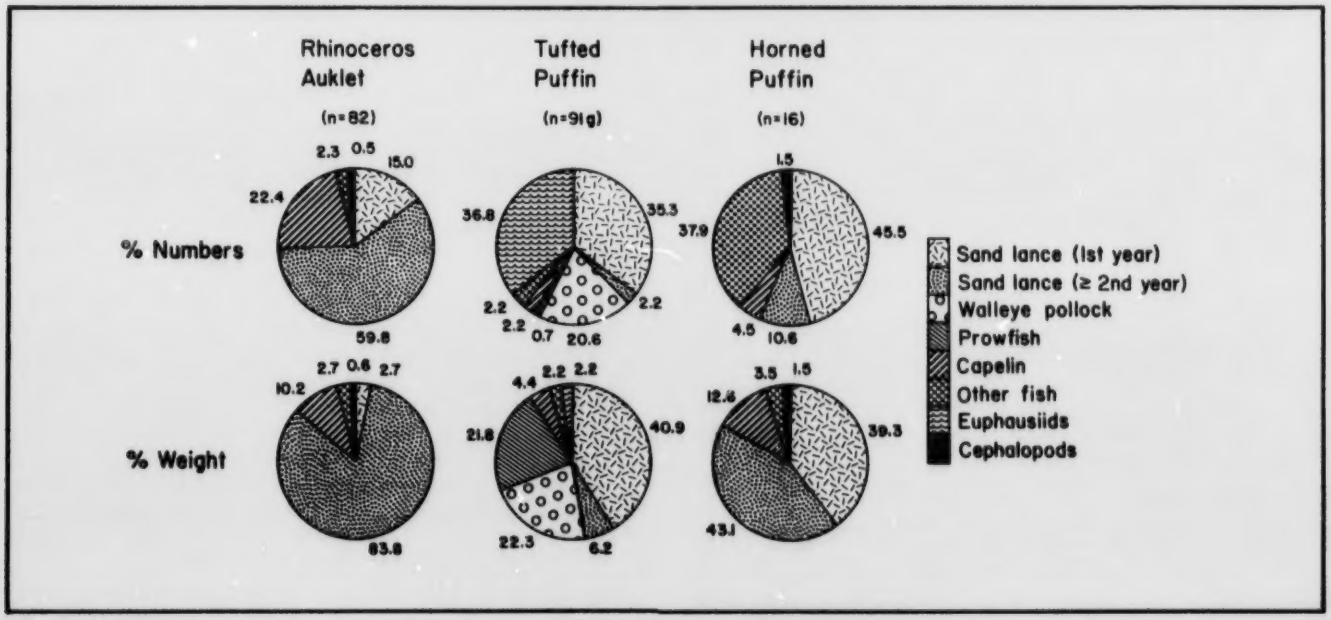


Figure 4
Nestling diets of Rhinoceros Auklets, Tufted Puffins, and Horned Puffins at the Semidi Islands, 18 July – 11 August 1979. Samples are burrow-loads for Rhinoceros Auklets, bill-loads for Horned Puffins, and pooled material from various sources for Tufted Puffins



Two distinct size-classes of sandlance were present in the food samples (Figs. 6 and 7), and their relative importance differed markedly between species and between study areas (Figs. 3 and 4). According to Blackburn (1979), the smaller fish (first-year) would have hatched within the current year, probably in January or February, whereas most of the larger fish (second-year) were hatched a year earlier. The two largest fish (150–170 mm) collected at Middleton Island were probably 3–5 years old, and this group seemed well represented at the Semidis.

Measurable growth occurred in the youngest sandlance during the sampling period at each site (Figs. 6 and 7). The rate of increase in mean body length was estimated by linear regression to be 18.7 mm per month at Middleton Island and 21.0 mm per month at the Semidis ($P < 0.001$ for both regressions, $r = 0.554$ and 0.768, respectively). These rates did not differ significantly, as shown by an analysis of covariance ($P = 0.225$). When age-classes are compared between the two sites, however, differences in overall mean length are evident in first-year and older fish alike (Fig. 8).

6.4. Analysis of variation in feeding rates

6.4.1. *Heterogeneity of load-sizes* — There was much variation in the weight of burrow-loads collected on a given night and in mean load weights on different nights (Fig. 9). A nested analysis of variance, with corrections for unequal sample sizes on different nights (Sokal and Rohlf 1981: 293), indicated that 60–80% of the variation in load-sizes occurred within nights, but about 20% occurred between nights (Table 3). No additional component of variance between sampling periods was found to account for variation between nights. However, because a seasonal increase in feeding rates occurred (see below), significant variation between periods would be evident had more sampling periods been included.

6.4.2. *Factors affecting feeding rates* — A number of factors might contribute to variation in feeding rates, including: (1) the age of the chick; (2) annual and seasonal changes in food availability; and (3) environmental variables such as wind or tides. The prevalence of sandlance in the diet of Rhinoceros Auklets suggests the composition of samples is usefully characterized by the proportion of sandlance per load and the relative proportions of the two size-classes. Since prey other than sandlance were scarce at both study areas, and many loads at the Semidis contained only second-year or older fish, skewness in the distributions of these variables was not eliminated by transformation. I excluded, therefore, samples consisting entirely of sandlance or entirely of second-year fish from the following correlation analysis.

Simple correlation coefficients between burrow-load-size and several of the above variables indicate that none of the relationships is particularly strong (Table 4). Most are statistically significant, however, and I would expect factors causing feeding rates to vary by 5–10% to have biological significance as well. Table 4 also reveals significant correlations among independent variables which could lead to spurious conclusions about their individual effects on load-size. At the Semidi Islands, for example, sampling date was strongly correlated with the ages of chicks in the sample. When the apparent effect of sampling date on load-size is removed by partial correlation, there still is a significant positive relationship with the age of the chick, but the reverse is not true (Table 5). Thus, the size of burrow-loads increased with the age of the chick, but no seasonal trend in food availability can be inferred.

The proportion of sandlance per load and the relative amounts of the two size-classes were correlated with sampling date and the age of the chick (Table 4). Here again, partial correlations, in which the effects of sampling date and chick-age were controlled, revealed these relationships to be real (Table 5). This conclusion is strengthened by a comparison of means between samples consisting entirely of sandlance and those containing other prey. Pure loads of sandlance averaged 41.8 g at Middleton and 40.8 g at the Semidis, compared with 35.6 g and 33.3 g, respectively, for loads of mixed species composition ($P < 0.10$ in each case, t-tests). Similarly, loads containing only large sandlance averaged 7.7 g heavier than loads containing both age-classes at the Semidis (41.1 *vs* 33.4 g, $P < 0.15$).

The relation observed at Middleton Island between chick-age and the relative proportions of large and small sandlance was highly significant ($P < 0.01$), even when all

Table 2
Prey species and their percent frequency of occurrence in food samples

	Middleton Island		Semidi Islands		
Species	**Rhinoceros Auklet** ($n = 68$)	**Tufted Puffin** ($n = 16$)	**Rhinoceros Auklet** ($n = 82$)	**Horned Puffin** ($n = 16$)	**Tufted Puffin** ($n = 91$)
Pacific sandlance					
First-year	92.6	75.0	29.3	63.6	present
Second-year	92.6	37.5	89.0	36.4	present
All ages	92.6	81.3	92.7	81.8	present
Capelin			47.6	18.2	present
Larval Osmeridae				9.1	
Pacific sandfish (*Trichodon trichodon*)	11.8	6.3			
Kelp greenling (*Hexagrammos decagrammus*)	10.3				
Unid. Hexagrammidae			12.2		
Prowfish (*Zaprora silenus*)		12.5			present
Sablefish (*Anoplopoma fimbria*)	4.4				
Walleye pollock					present
Rockfish (*Sebastes* sp.)	7.4		3.7		present
Larval Pleuronectidae					present
Squid (*Gonatus middendorfi*)	7.4	43.8	4.9		
Octopus (*Octopus* sp.)	7.4	43.8		9.1	
Euphausiidae					present

Figure 6
Length frequency distributions of Pacific sandlance in the diet of Rhinoceros Auklet nestlings, Middleton Island, 1978. Fish in the stippled area were assigned to the first-year age-class; fish in the unshaded area were considered second-year or older

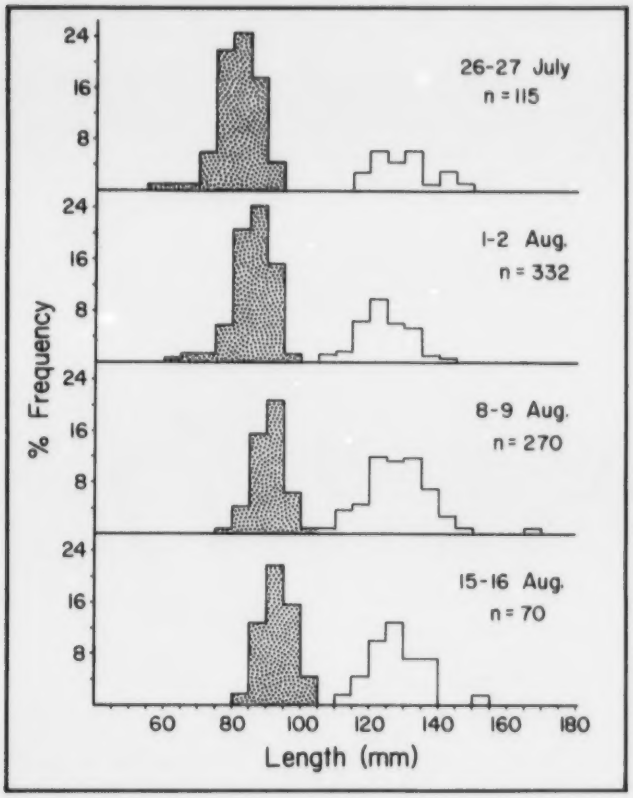
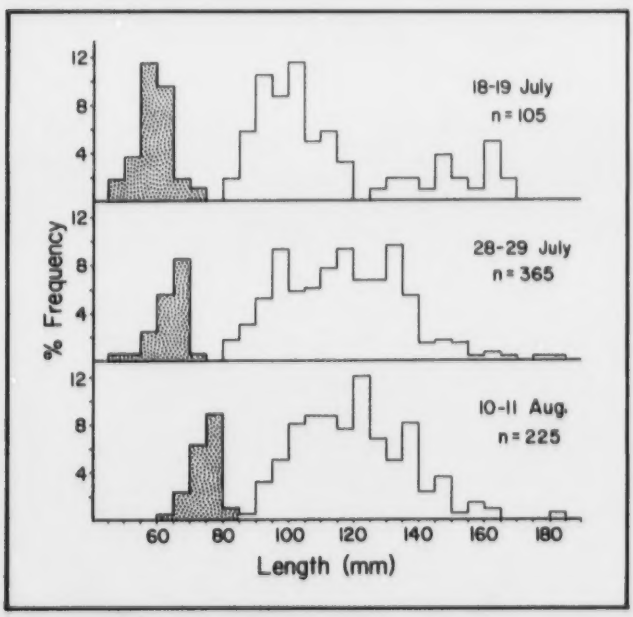


Figure 7
Length frequency distributions of Pacific sandlance in the diet of Rhinoceros Auklet nestlings, Semidi Islands, 1979. Fish in the stippled area were assigned to the first-year age-class; fish in the unshaded area were considered second-year or older

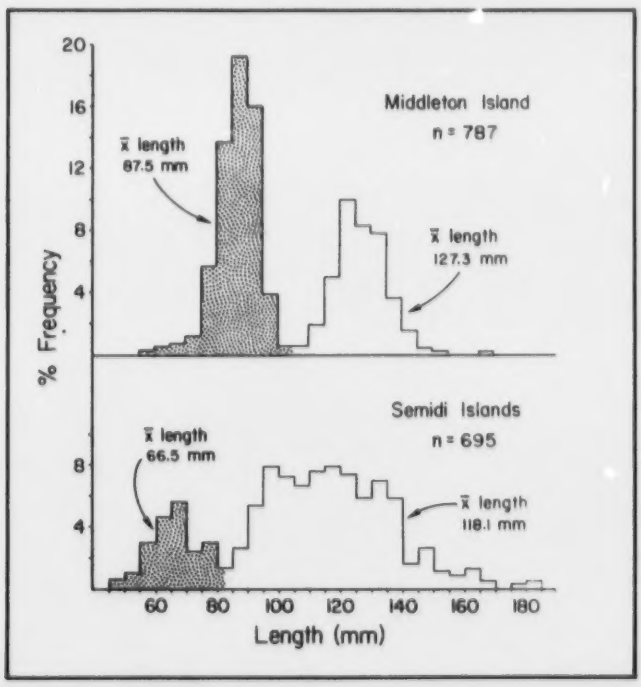


other variables (load-size, sampling date, and percent total sandlance) were controlled. Thus, a tendency for parents of older chicks to deliver larger fish selectively appears to be real.

6.4.3. *Heterogeneity in species and age composition of burrow-loads* — Since load-size was correlated with species composition and the proportional amounts of first-year and older sandlance, I examined variability in these characteristics in relation to samples collected on the same night, on successive nights, and in different sampling periods. Chi-square tests for heterogeneity of species composition within nights are limited to three nights at the Semidi Islands when substantial numbers of prey other than sandlance (mostly capelin) appeared in the samples. When capelin were available, they did not occur uniformly in all samples, but tended to show up disproportionately in a few (Table 6). Similarly, loads tended to consist of one age-class of sandlance or the other on nights when both classes were well represented (Table 7). One group or the other was largely absent on a few nights (dates excluded from the analysis).

Because both aspects of load composition varied significantly within nights, I used the nonparametric Kruskal-Wallis analysis of variance to test the significance of variation between nights and between sampling periods. Species composition (Table 6) was expressed as the percentage (by weight) of sandlance in each sample and age composition (Table 7) as the proportion of second-year or older sandlance. Again, there was significant heterogeneity in these characteristics between samples collected on successive nights and among samples collected during different stages of the season. The percentage of tests in which the

Figure 8
Comparison of length frequencies of Pacific sandlance in food samples from Middleton Island, 1978, and the Semidi Islands, 1979. Fish in the stippled area were assigned to the first-year age-class; fish in the unshaded area were considered second-year or older



null hypothesis is rejected is less than for samples collected on the same night, just as most variation in load-sizes occurred within nights (Table 3).

6.4.4. *Influence of weather on feeding rates* — One additional factor that may influence feeding rates is wind and associated sea conditions. Fortuitously, each sampling period at the Semidi Islands included one windy and one calm night (Fig. 9*b*). On windy nights, wind velocity varied between about 20 and 50 km/h. For this analysis I treated wind as a nonmetric variable with two categories, windy or calm. I used an analysis of covariance to control for the increase in feeding rate as chicks aged. Results indicated that wind reduced mean load-size by about 11 g overall, a highly significant effect (Table 8).

My record of weather at Middleton Island is incomplete, but wind speeds varied little, probably averaging between 10 and 20 km/h each night. Nevertheless, there was as much variation in mean load-size between nights on Middleton as at the Semidis (Fig. 9, Table 3), so the influence of wind speed on feeding rates remains uncertain.

7. Discussion

7.1. Feeding rates: means and variability

Studies of Rhinoceros Auklets in Washington (Richardson 1961, Cody 1973, Leschner 1976, Wilson 1977) and British Columbia (Vermeer *et al.* 1979) found mean bill-load weights in the range 29–37 g, though Leschner observed a mean of 19 g in 1 of 2 years. The average burrow-loads observed in my study are close to what one would expect if chicks were fed by one adult each night. Whether this was so or whether two adults brought smaller than usual bill-loads is not known. Thirty-three of 68 burrow-loads (49%) collected on Middleton Island and 32 of 82 burrow-loads (40%) collected at the Semidis weighed more than 40 g and probably included two deliveries.

Table 3
Composition of the variance in weight of burrow-loads illustrated in Figure 9

	Middleton Island		Semidi Islands	
Source of variation	% of total variation	*P*	% of total variation	*P*
Between sampling periods	0.6	0.466	17.7	0.240
Between nights, within sampling periods	21.4	0.016	20.1	0.002
Within nights, between individuals	78.0		62.2	

Table 4
Pearson correlation coefficients among load-size and several independent variables. All values above the diagonal are for Middleton Island; values below are for Semidis

		Weight of load	Age of chick	Sampling date	% total sandlance	% large sandlance*
Weight of load	*r*		0.066	0.055	0.332	0.411
	df	—	66	66	23	66
	P		0.295	0.329	0.048	<0.001
Age of chick	*r*	0.344		0.320	0.096	0.339
	df	80	—	66	23	66
	P	0.001		0.004	0.324	0.002
Sampling date	*r*	0.235	0.729		0.135	0.300
	df	80	80	—	23	66
	P	0.017	0.001		0.260	0.006
% total sandlance	*r*	0.634	0.283	0.368		0.145
	df	41	41	41	—	21
	P	<0.001	0.033	0.008		0.254
% large sandlance*	*r*	0.361	−0.079	−0.188	0.648	
	df	24	24	24	18	—
	P	0.035	0.351	0.178	0.001	

*Weight of large sandlance as a percentage of total sandlance in the load.

Table 5
Partial correlations of load-size with selected variables from Table 4

Area	Correlated variable	Variables controlled	*r*	df	*P*
Middleton	% total sandlance	Age of chick, sampling date	0.343	21	0.050
	% large sandlance	Age of chick, sampling date	0.417	64	<0.001
Semidis	Age of chick	Sampling date	0.260	79	0.010
	Sampling date	Age of chick	−0.036	79	0.379
	% total sandlance	Age of chick, sampling date	0.604	39	<0.001
	% large sandlance	Age of chick, sampling date	0.426	22	0.019

Table 6
Heterogeneity of Rhinoceros Auklet food samples with respect to the proportion of sandlance per load

Area	Source of variation	Test	Date(s)	χ^2	df	*P*
Middleton	Between nights (within periods)	Kruskal-Wallis	26–27 July	4.7	1	0.031
			1–2 Aug.	5.6	1	0.018
			8–9 Aug.	1.4	1	0.233
			15–16 Aug.	0.1	1	0.748
	Between sampling periods	Kruskal-Wallis	26 July – 16 Aug.	9.7	3	0.021
Semidis	Between samples (within nights)	Chi^2	18 July	12.4	5	0.030
			19 July	67.9	14	0.001
			29 July	48.2	14	0.001
	Between nights (within periods)	Kruskal-Wallis	18–19 July	0.01	1	0.901
			28–29 July	3.5	1	0.063
			10–11 Aug.	0.3	1	0.577
	Between sampling periods	Kruskal-Wallis	18 July – 11 Aug.	23.4	2	0.001

The quantity of food delivered daily increased with the age of the nestling. Harris (1978) and Ashcroft (1979) showed that the rate of food consumption in Atlantic Puffins increased with age to a point, then declined during the last 2 weeks of the nestling period. No such pattern is evident in my data for Rhinoceros Auklets, but older nestlings may have been inadequately sampled. I assumed the relationship to be linear.

Additional variation in feeding rates presumably reflected changes in prey availability. Variation occurred both within and between nights, as did changes in the relative amount and size distribution of sandlance in the samples. My interpretation is that movements of this prey species, particularly the older individuals, largely determined the foraging success of Rhinoceros Auklets. When second-year and older sandlance became temporarily unavailable, the birds apparently were unable to compensate by switching to alternate prey.

7.2. Inferences about the population biology of sandlance

Recognizing that burrow-loads probably consisted of one or two bill-loads, I believe that strong heterogeneity in the composition of samples within nights simply resulted from small-scale patchiness in the distribution of prey. Birds probably encountered fish in fairly uniform shoals. Presumably, however, variation between nights and between sampling periods resulted from more pervasive temporal shifts in prey availability.

Carefully interpreted, the correlations shown in Tables 4 and 5 indicate age-specific patterns of movement and availability in sandlance. An increase in the proportion of large sandlance in the diet could come about in three ways. First, an increase in the absolute availability of large sandlance would increase load-size, total sandlance per load, and the relative proportion of large sandlance. Second, a decrease in the availability of small sandlance would increase the proportion of large fish, but total sandlance and load-size would decrease. Third, compensatory shifts could occur such that total biomass of sandlance remains the same but

Figure 9
Variation in the weight of burrow-loads of Rhinoceros Auklets: (*a*) Middleton Island, 1978; and (*b*) Semidi Islands, 1979, showing associated weather conditions

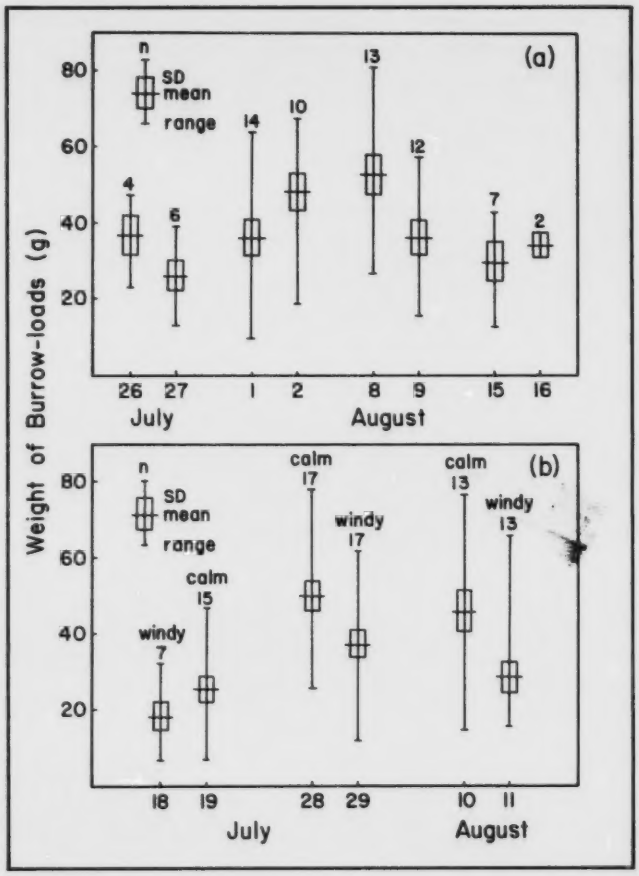


Table 7
Heterogeneity of Rhinoceros Auklet food samples with respect to the proportions of small and large size-classes of sandlance

Area	Source of variation	Test	Date(s)	χ^2	df	*P*
Middleton	Between samples (within nights)	Chi^2	26 July	21.5	3	0.001
			1 Aug.	66.1	13	0.001
			2 Aug.	44.0	9	0.001
			8 Aug.	37.9	12	0.001
			9 Aug.	32.5	11	0.001
			15 Aug.	2.5	6	0.871
			16 Aug.	10.3	1	0.005
	Between nights (within periods)	Kruskal-Wallis	26–27 July	2.3	1	0.130
			1–2 Aug.	0.01	1	0.907
			8–9 Aug.	5.0	1	0.026
			15–16 Aug.	0.0	1	1.000
	Between sampling periods	Kruskal-Wallis	26 July – 16 Aug.	6.5	3	0.091
Semidis	Between samples (within nights)	Chi^2	19 July	49.3	10	0.001
			29 July	85.7	14	0.001
			11 Aug.	82.0	12	0.001
	Between nights (within periods)	Kruskal-Wallis	18–19 July	2.1	1	0.149
			28–29 July	6.1	1	0.013
			10–11 Aug.	1.4	1	0.236
	Between sampling periods	Kruskal-Wallis	18 July – 11 Aug.	10.4	2	0.005

the relative abundance of large fish increases. In that situation, load-size and total sandlance would remain constant as the proportion of large fish increased. The results in Table 5 are consistent only with the first of these alternatives. The observed correlations apparently resulted from changes in the availability of second-year and older sandlance. Either the availability of first-year fish did not vary appreciably, or this variation exerted little influence on foraging success.

There was little difference between growth rates of first-year sandlance at Middleton Island and the Semidis. Furthermore, although sampling occurred 6 days earlier at the Semidis, that cannot account for the difference in size of first-year fish at the two study sites (Fig. 8). Therefore a difference in spawning time is the most likely explanation. The difference in the breeding phenology of puffins at the two sites paralleled this apparent difference in the phenology of their principal prey.

Judging from their greater abundance in food samples, second-year and older sandlance were more available at the Semidi Islands than at Middleton. I would expect this to affect the foraging success of Rhinoceros Auklets, yet feeding rates were similar at the two sites. The conclusions possible from a geographical comparison, however, are limited on this point. A longitudinal study at one site would be better because the ratio of age-classes in food samples provides no information about their absolute abundance, and we do not know the areas over which populations of sandlance are relatively discrete. The demography of sandlance is probably well represented, however, by sampling at one locality through time.

7.3. Differentiation of food habits among puffins

A salient result of this study is the degree to which Rhinoceros Auklets diverged from the other species in exploiting mainly older age classes of sandlance. Presumably this relates to the depth or distance from the colony at which the species feed, or to their differing daily activity schedules. (Rhinoceros Auklets deliver food to the young only at night, when the distribution of sandlance may be different than in daylight.) The populations of many pelagic fish are characterized by having relatively strong and weak year-classes resulting from large annual fluctuations in reproductive success (May 1974, Ricker 1975). Sandlance, at least in the North Sea, are no exception (Hart 1974). Whether the age-structure of prey populations differentially affects the breeding performance of puffin species would be interesting to explore. My data indicate that such an effect is likely, but the proper study of this phenomenon requires several years' observations on food habits and breeding success at mixed colonies. I expect the effect to be most evident where puffins exploit few species of prey, as appears to be true in the Gulf of Alaska.

Table 8
Composition of the variation in weight of burrow-loads explained by wind speed and age of the chick, Semidi Islands, 1979

Source of variation	% of total variation	*P*
Additive effects of chick-age and wind	21.5	0.001
(i) Wind, adjusted for chick-age	8.8	0.012
(ii) Chick-age, adjusted for wind	12.7	0.001
Interaction	2.8	0.093
Residual	75.7	

8. Acknowledgements

The work on Middleton Island was supported by the Bureau of Land Management through interagency agreement with the National Oceanic and Atmospheric Administration, under which a multi-year program responding to needs of petroleum development of the Alaskan continental shelf is managed by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) Office, Juneau. I thank Thomas Pearson for field assistance on Middleton Island and my wife, Martha Hatch, for helping at the Semidis. Martha Wiley and Rena Wenkart sorted the food samples collected on Middleton Island. Cephalopods were identified by Chris Bublitz; William Colgate identified the euphausiids. The manuscript benefited from the reviews of Gerald Sanger, David Ainley, Robert Furness, Spencer Sealy, Calvin Lensink, and Lynne Krasnow.

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10. Appendix

Evaluation of the collecting technique

There were no obvious indications that the use of muzzles on nestling Rhinoceros Auklets interfered with normal food provisioning by their parents, but further studies should include direct observations on marked burrows as a control. The technique caused the loss or injury of some chicks at Middleton, but this was eliminated with the use of cloth muzzles at the Semidis (Table 1).

In contrast, the method had a clear and immediate effect on the parental behaviour of Tufted Puffins, although the reasons for this difference are not clear. Mean load-size was depressed, and in most cases feeding ceased altogether. The parents must often have eaten the first bill-loads they brought after the chicks were muzzled, otherwise I would have found at least some food in most burrows. Feeding continued at undisturbed burrows on Middleton Island, and 10 control chicks grew normally throughout the season. Nearly total mortality occurred among Tufted Puffin chicks muzzled at the Semidi Islands, so the procedure was soon discontinued. Chicks that disappeared had apparently wandered out of their burrows. Although further trials with Horned Puffins are needed, it appeared that problems similar to those encountered in Tufted Puffins can be expected. If the technique caused subtle changes of parental behaviour in Rhinoceros Auklets, this would not necessarily alter any of the conclusions I have drawn, beyond the estimation of overall feeding rates.

Chairmen: David N. Nettleship
George L. Hunt, Jr.
Alec D. MacCall

Part III

Seabird – commercial fisheries interactions

Modelling relationships among fisheries, seabirds, and marine mammals

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1. Abstract

Calls for culls of seals or seabirds to increase fishery yields have been based on the projection of captive studies of food intake to field populations. Such estimates make a number of unsupported assumptions and lack statistical confidence limits. More precise computations can be made, based on generalized bioenergetics equations. Modelling indicates that seabirds in several ecosystems consume 20–30% of annual pelagic fish production, so are potentially in competition with commercial fisheries. Such estimates require sound knowledge of population size and flux, activity budgets, foraging ranges, and diets as well as data on fish production. Detailed studies of single-species populations could be used to validate the results of bioenergetics modelling. However, partitioning fish consumption between competing interests does not in itself allow detailed predictions of changes that will result from human manipulation. A number of empirical studies indicate that population responses to a reduced food supply depend on a spectrum of factors, particularly species life history and interspecific relationships.

2. Résumé

Les demandes d'abattage de phoques ou d'oiseaux de mer pour accroître le rendement de la pêche s'appuient sur la transposition d'études sur l'ingestion d'aliments en captivité à des populations sauvages. Ces estimations posent un certain nombre d'hypothèses non vérifiées et sont dépourvues de limites de confiance statistiques. Il est possible de faire des calculs plus précis en s'appuyant sur des équations généralisées de bioénergétique. La modélisation révèle que les oiseaux de mer de plusieurs écosystèmes consomment 20 à 30 % de la production annuelle de poissons pélagiques, ce qui en fait des concurrents potentiels pour la pêche commerciale. Ce genre d'estimation nécessite une parfaite connaissance de la taille des populations et de leurs mouvements, des budgets d'activité, de la distribution des aires d'alimentation et des régimes alimentaires ainsi que des données sur la production de poissons. Des études détaillées sur les populations à espèce unique pourraient servir à confirmer les résultats de la modélisation bioénergétique. Toutefois, le partage de la consommation de poissons entre les divers intérêts en jeu ne permet pas comme tel de prédire fidèlement les changements qui résulteraient de l'intervention humaine. Un certain nombre d'études empiriques révèlent que les réactions des populations à une réduction de l'approvisionnement alimentaire dépendent de toute une gamme de facteurs, en particulier du cycle biologique des espèces et des rapports interspécifiques.

3. Introduction

This paper reviews the usefulness and limitations of quantitative estimation of the energy requirements of seabird and marine mammal populations, as a step towards understanding the interactions between these predators and their prey populations, and outlines the complex ecosystem relationships that need to be elucidated in order to allow the construction of models capable of predicting effects of perturbations of fish stocks on their natural predators.

Increasing human exploitation of fish stocks throughout the world has led to a focusing of attention on the management of marine ecosystems to maximize their yield to people. Rather than treating each fish population as if it were an isolated stock, as earlier fisheries biologists tended to do, it has become clear that we must manage whole ecosystems in order to optimize the yields of different commercially valuable organisms. Recent investigations of fisheries and stock changes have demonstrated the importance of competition and predator–prey interactions among species of fish (Andersen and Ursin 1977), and revealed management problems involving interactions between several trophic levels (May *et al.* 1979). Seabirds and marine mammals are often top predators in marine ecosystems, and as such are potential competitors with commercial fisheries. Where it is believed that this competition may result in serious and avoidable financial loss to commercial fisheries, an assessment of economic impact of seabirds and seals is a prerequisite to sensible management. Such assessment is most easily made by estimating the population energy requirement, and converting this to food consumption from information on the composition of the diet.

A knowledge of the quantities of food consumed by seabirds and marine mammals is also useful in the search for causal relationships between changes in marine ecosystem structure, induced by environmental changes or overfishing, and changes in the sizes of seabird and mammal populations. With increasing utilization of marine resources there have been demonstrable changes in the structure of many marine ecosystems, and these will inevitably influence populations of non-target species through alterations in the availability, quantity, or quality of their food supplies.

Although we are able to estimate the food consumption of populations, construction of models to simulate the effects of food shortage on seabird population biology is a

much more difficult task. I shall discuss this problem after reviewing the simpler energetics studies.

4. Energy budgets

Broadly speaking, the approaches to quantifying the food consumption of seabird and marine mammal populations can be separated into three groupings, of increasing precision:

1. Combination of population census data with studies of food consumption by captive, or sometimes, free-living, animals;

2. Construction of simulation models combining population data and bioenergetic equations derived by controlled laboratory experimentation; and

3. Direct measurement of metabolic rate in free-living animals. I shall consider the use of these methods for estimating population food consumption (1) by marine mammals and (2) by seabirds.

4.1. Marine mammal energy budgets

4.1.1. *Combination of census data and captive feeding studies* — The controversial proposals to cull grey seals (*Halichoerus grypus*) at colonies around Britain provide a good example of the approach used to estimate the quantity of exploited fishery resources consumed by seals and the consequential loss of potential fishery catch. Annual consumption of each prey species by the seal population is estimated from three sets of data: (1) the total number of seals of all ages in the population; (2) the average quantity of food consumed per seal per day; (3) the proportion, by weight, of each species in the diet.

Adult grey seals cannot be counted at sea or at breeding colonies as they are never all together, and the proportion present at any particular time is unknown. The size of the population has to be estimated from counts of pups and life-table statistics (Summers 1978). The ratio of pup numbers to total population size depends on adult survival rate, fecundity, juvenile survival rate, neo-natal mortality, time spent ashore by pups before putting to sea, and the extent of the breeding season. Detailed life-table data are available only for the increasing Farne Islands population, and conversion of pup counts to population size for other areas extrapolate from the Farnes data, assuming that these mortality and fecundity data are applicable to the other populations. The validity of this procedure is dubious, and it is not possible to attach confidence limits to the estimates of total population size. It can be suggested that the mid 1970s pup production of 19 000 individuals at British colonies represents a population size of 70 000 animals, and comparisons with earlier counts indicate a 6–7% increase per annum (Summers 1978).

With presently available techniques, the daily food intake of seals cannot be measured in the field. Such studies would be almost impossible to conduct owing to the pelagic distribution of seals outside the breeding season. Owing to their rapid digestion of food, analysis of stomach contents cannot give reliable information on feeding rates, although this may give an indication of maximum meal size. The assessment of food consumption has been limited to studies of seals kept in captivity. A detailed survey of pinniped species kept in captivity recorded daily food intake of 6–10% of body weight (Keyes 1968), and similar results have been obtained for porpoises (Sergeant 1969). Rae (1960) and Parrish and Shearer (1977) used an average value of 7 kg per grey seal per day, applying for every day of the year, for the total, all-age, population of grey seals breeding in the British Isles. This was based on observed intake in captivity, and is at the lower end of the range 6–10% of mean body weight. However, grey seals fast for up to 6 weeks during the breeding season, and lose weight, and it is debatable whether captive feeding rates can be applied to wild animals, which are likely to be more active than those in captivity and are less likely to overeat.

4.1.2. *Use of bioenergetics equations for marine mammals* — Grenfell and Lawton (1979) used bioenergetics equations provided by Lockyer (1976) to estimate resting metabolic rates (*RMR*) of marine mammals from their body weights. Lockyer (1976) obtained the relationship:

$$RMR \text{ (kcals/day)} = 126.2\, W^{0.77} \text{ (SE } 0.035)$$

(where W is body weight in kg, 1 kcal = 4.19 kJ) from studies using a variety of whales and seals. To convert this to field metabolic rates (*FMR*) Grenfell and Lawton (1979) multiplied *RMR* by a factor of 2, with lower limit of 1.5 and upper limit of 3. Hinga (1979) concluded that the field energy requirements of large whales are approximately 1.5 times *RMR*.

To *FMR* must be added costs of tissue production and assimilation. Humphreys (1979) found an average annual production by large mammals equalling 3.4% of energy assimilation. Assimilation efficiency (conversion of food ingested into assimilated energy) is about 80% in most carnivorous mammals (Lawton 1970). Using Grenfell and Lawton's method, the energy requirement of a grey seal weighing 110 kg would be 12 000 kcals/day, equivalent to about 11 kg of fish/day, if a conversion factor of 2 is used to obtain *FMR* from *RMR*. This suggests that the 7 kg/day estimated from captive feeding studies may be a conservatively low value when calculating total food intake by the population.

4.1.3. *Estimated impacts of grey seals on fish stocks* — Grey seal diet has been examined by stomach sampling from animals caught by or in the vicinity of nets or whitefish boats, mainly along the Scottish east coast. This doubtless biases the data in favour of commercially exploited fish species. Little is known of the seasonal or geographical variation in grey seal diet, but it seems likely that cephalopods and sandlance (*Ammodytes marinus*) are important in the diet of grey seals in Orkney and Shetland, where very little stomach sampling has been attempted (Rae 1960). Fishery biologists have tended to discount this bias as insignificant, but in fact it is an unknown and possibly very considerable one.

The final problem is estimation of the loss of potential fishery catch. This can be estimated given the exploitation rate of the fishery for each species consumed and on the assumption that the fish consumed would, if not eaten, be available to the fisheries in the same manner as those not subject to seal predation. For most fish stocks in British waters the rate of exploitation (defined as fishing mortality rate/total mortality rate) is high, in excess of 0.5, and stocks are depleted as a result. Of course, a proportion of the grey seal's diet will be small fish not yet recruited into the commercial fishery and this cannot be adequately assessed at present owing to the biased nature of stomach samples collected to date and to the tendency for much of the stomach contents to be partly digested.

As a result of all these uncertainties, no precise estimate of either the amount of fish consumed by grey seals or the loss of potential fishery catch can be made. Total population size and mean body weight are unlikely to be in error by as much as 50%, but daily food intake may be at least 50% more or less than estimated, and dietary composition of all grey seals throughout the whole year may be very different from that of the samples collected. In view of this, it is little more than speculation to use these data to calculate the impact of grey seals on British fisheries, but Parrish and Shearer (1977) nonetheless suggested that fish consumption by grey seals amounted to 112 000 t/year, and that this, according to the available dietary information, represented a loss of catch to the fishing industry in the mid 1970s of 56 000 t, equivalent to US$30 million and 5–10% of the total fish catch taken within the UK's fishery limits.

4.2. Seabird population food requirements

4.2.1. *Field estimation of seabird food consumption* — In many seabird communities one or two species are numerically dominant and are also responsible for almost all the food consumption of the community. Field observations show how many feeding trips each adult makes per day and how much food is carried in an average meal. Multiplication of these by the number of adults and the number of days that the birds spend at the colony each summer gives the food consumption by the population over the breeding season. Many practical difficulties arise with this method. For example, numbers of feeding trips per day vary seasonally and in relation to brood size and chick age. Non-breeders spend only part of the summer at the colony and take less food than breeders. Even so, this direct approach has been used in a number of early attempts to quantify food consumption by seabirds, particularly with large colonies of Common Murres (*Uria aalge*) and Thick-billed Murres (*Uria lomvia*). At the Seven Islands Reserve, Murman coast, Barents Sea, Kaftanovski (1951) estimated adult food intake at 30 g/day. Also on the Murman coast, Belopolskii (1961) estimated adult food consumption at about 60 g/day and chicks' consumption at 20 g/day. On Novaya Zemlya, Uspenski (1956) calculated that adults take 100 g/day and chicks 35–40 g/day, while Tuck and Squires (1955) at Akpatok Island, Ungava Bay, estimated that adults ate 220 g/day and, from feeding experiments, determined that chicks consumed 13.4 g/day for each gram increase in body weight, or the equivalent of about one-half their body weight in food per day. Although some of the differences between these estimates may be due to variations in climate, food availability, adult activity budgets, or the calorific value of the food taken, such empiric calculations of food consumption are clearly only able to provide an order of magnitude estimate for the food consumption of the seabird communities studied by these authors.

4.2.2. *Bioenergetics models* — The use of bioenergetics equations is reviewed by Kendeigh *et al.* (1977) and the application of bioenergetics modelling in estimating the potential impact of granivorous passerines on the ecosystem is reviewed by Wiens and Dyer (1977). Bioenergetics modelling aims to obtain the values for the numerous parameters of breeding biology and to couple these with generalized bioenergetics equations, computed for passerines or non-passerines, to calculate the daily energy budget of a population. Thus, values obtained under controlled laboratory conditions are projected to free-living populations with specified activity patterns, biology, and environment. The extensive literature on seabird populations and biology makes this an obvious approach to adopt when considering their impact on fish stocks.

Metabolism can be most precisely defined and measured in terms of the basal metabolic rate (*BMR*). This is the rate of energy utilization by animal tissues at rest and unstimulated by food assimilation or digestion or by low or high temperature. In the field, animals never exist at their *BMR*, as they are usually digesting food and not at complete rest, so basal metabolism is not appropriate for bioenergetics modelling. A more useful measure is "existence metabolism" (*EM*). This is defined as the rate of energy utilization by caged birds able to undertake limited locomotor activity (but not flight) and that are maintaining a constant mass and not undergoing reproduction, moult, growth, or migratory restlessness. Kendeigh (1970) gave logarithmic allometric equations for *EM* of 13 passerine and 5 non-passerine species. Within these categories species followed a common relationship, implying that the *EM* of any seabird species can be calculated from a knowledge of its mass, and the ambient temperature.

Wiens and Scott (1975) based their simulation of Oregon seabird energetics on Kendeigh's equations derived from studies of five non-passerines (a duck, a goose, and three pheasant species). I also used these equations as the basis of a simulation of a Shetland seabird community energy budget (Furness 1978), but pointed out the wide confidence interval associated with Kendeigh's equations, such that these provided the main source of error in the model. Since 1970, extensive studies of *EM* have been carried out with a wide variety of species. Kendeigh *et al.* (1977) confirmed the differences between passerines and non-passerines, and showed that the relationships were identical for almost all orders of non-passerines. Based on 40 or more species of non-passerine the regressions have much smaller standard errors than those used by Wiens and Scott (1975) or Furness (1978). For a typical seabird this would be about 1% rather than the 15–25% resulting from the Kendeigh (1970) equations. Allometric equations have also been derived for other activities of free-living birds, so that activity budget data may be converted to energy expenditure (Kendeigh *et al.* 197?).

The activities likely to make the most substantial contributions to seabird population energy budgets are foraging, provisioning of chicks, adult moult, and egg production. Energy costs of flapping flight have been accurately measured (Kendeigh *et al.* 1977). Energy costs of gliding flight and surface swimming have been determined for a small number of species and are about twice resting metabolism (Prange and Schmidt-Nielsen 1970, Baudinette and Schmidt-Nielsen 1974). No data are available for the costs of swimming or flying underwater, a feeding technique widely employed by seabirds. This provides a major potential error in the calculation of foraging costs. Furness and Cooper (1982) assumed that the costs of underwater swimming were similar to the costs of sustained flight. Given the uncertainties over the allocation of foraging time to different activities, such an assumption is unlikely to provide a major source of error in the modelling process, and it seems likely that both flapping flight and underwater foraging have similar energy costs close to the physiological maximum of which the bird is capable.

Chick energy budgets were computed by Kendeigh *et al.* (1977) from empirical data derived mainly from detailed studies of House Sparrows (*Passer domesticus*) and

Black-bellied Tree-ducks (*Dendrocygna autumnalis*). Regression of the daily energy budget on body mass of the young birds showed good agreement between species in spite of the wide variety of species and modes of development.

Adult moult costs depend on the mass of feathers replaced, which is proportional to body mass to the power 0.96 (Turcek 1966). Feather replacement in the House Sparrow costs 185 kcals per bird (Kendeigh *et al.* 1977) so the cost of moult may be approximated by the equation:

$$\text{Moult cost} = 8.3\ W^{0.96}\ \text{(kcals)}$$

where W is the body mass in grams. This is the only equation available for estimating seabird moult costs and is likely to be inaccurate as it is based on the study of a single passerine species. However, moult costs are a very small part of a seabird population energy budget (Williams *et al.* 1977, Furness and Cooper 1982).

The cost of egg production is calculated from the fresh mass of the egg at laying, the calorific value of the egg (averaging 1.3 kcals/g wet mass [King 1973, Schreiber and Lawrence 1976]) and the efficiency of egg production from body reserves, taken to be 73% (El-Wailly 1966, King 1973).

While it is desirable to have more precise knowledge of the energy costs of these various activities, the accuracy of a simulation model is limited not so much by these bioenergetics equations, but mainly by imprecisions in the estimates of seabird population sizes and the foraging activity budgets of adults (Furness and Cooper 1982).

The major inputs and computations for a typical model are shown in Figures 1*a–d*. Many inputs can be given with great precision. For example, chick weight in relation to age can be closely modelled by growth equations (Fig. 2). In contrast, some parameters are difficult to specify. Adult body weight is an important input, but may show dramatic seasonal variation (Fig. 3).

Model sensitivity can be explored by altering each input or bioenergetics parameter value in turn by 1% and recording the percentage change in the output estimate of total population energy requirement. Parameter sensitivity is defined as the percentage change in output value resulting from a 1% change on an input value. Almost all parameters have sensitivity values of considerably less than one (Figs. 4 and 5). Their exact magnitude depends to some extent on the biology of the species. The Skua (*Catharacta skua*) is a seabird with a fairly high body mass, which spends only a few hours foraging each day during its 5-month breeding season. The Arctic Tern (*Sterna paradisaea*) weighs less, spends only 3 months at the breeding site and at least one adult of each pair is foraging throughout most of the daylight period. In the case of the Skua the model is most sensitive to the estimation of existence metabolism, numbers of individuals in the population, and food utilization efficiency. For the Arctic Tern the model is most sensitive to the activity budget of adults, numbers in the population, and food utilization efficiency. Determination of sensitivity values should be carried out whenever this type of simulation modelling is undertaken as it indicates which parameters must be precisely known to give output results with small standard errors.

Model accuracy can be estimated by using a Monte Carlo technique (Furness 1978). Using the bioenergetics equations in Kendeigh *et al.* (1977) the 95% confidence interval for the model estimate of population energy requirement of Shetland or South African seabirds is about

Figure 1
Components of a seabird bioenergetics model: (*a*) population total comprises non-breeders, breeders, and chicks; (*b*) inputs for non-breeders; (*c*) inputs for breeders also include costs of egg production; (*d*) inputs for chicks. Note that refinements to include costs of moult, change in adult weight, or incubation have been ignored for simplicity

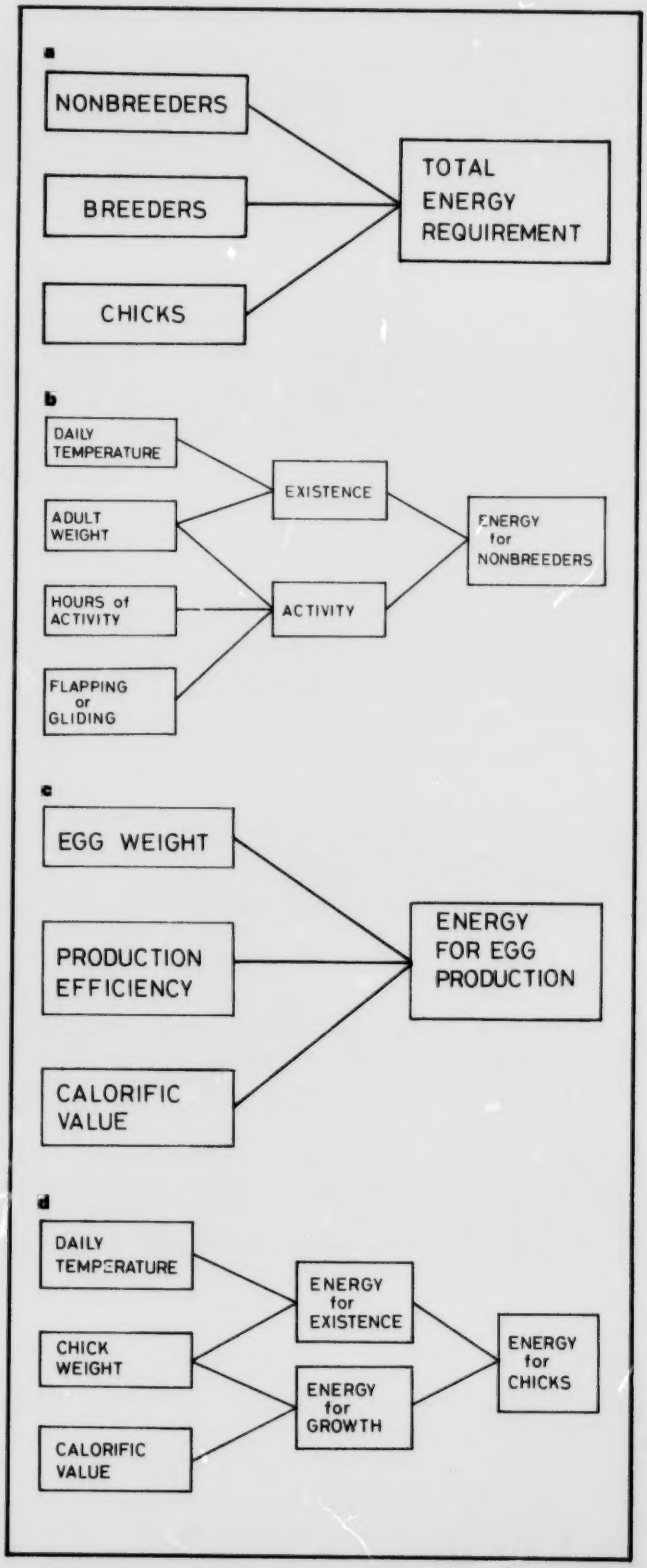


Figure 2
Growth of Skua chicks: mean weights (dots) and upper and lower 66% confidence intervals for individual weights (stars) are shown for 1255 measurements of chicks of known age hatched between 20 May and 20 June 1975. The line represents the logistic equation of best fit, used in bioenergetics modelling: $w = 1167.08/(1 + 16.955^{e-0.176t})$, where w is chick weight in grams and t is the age in days

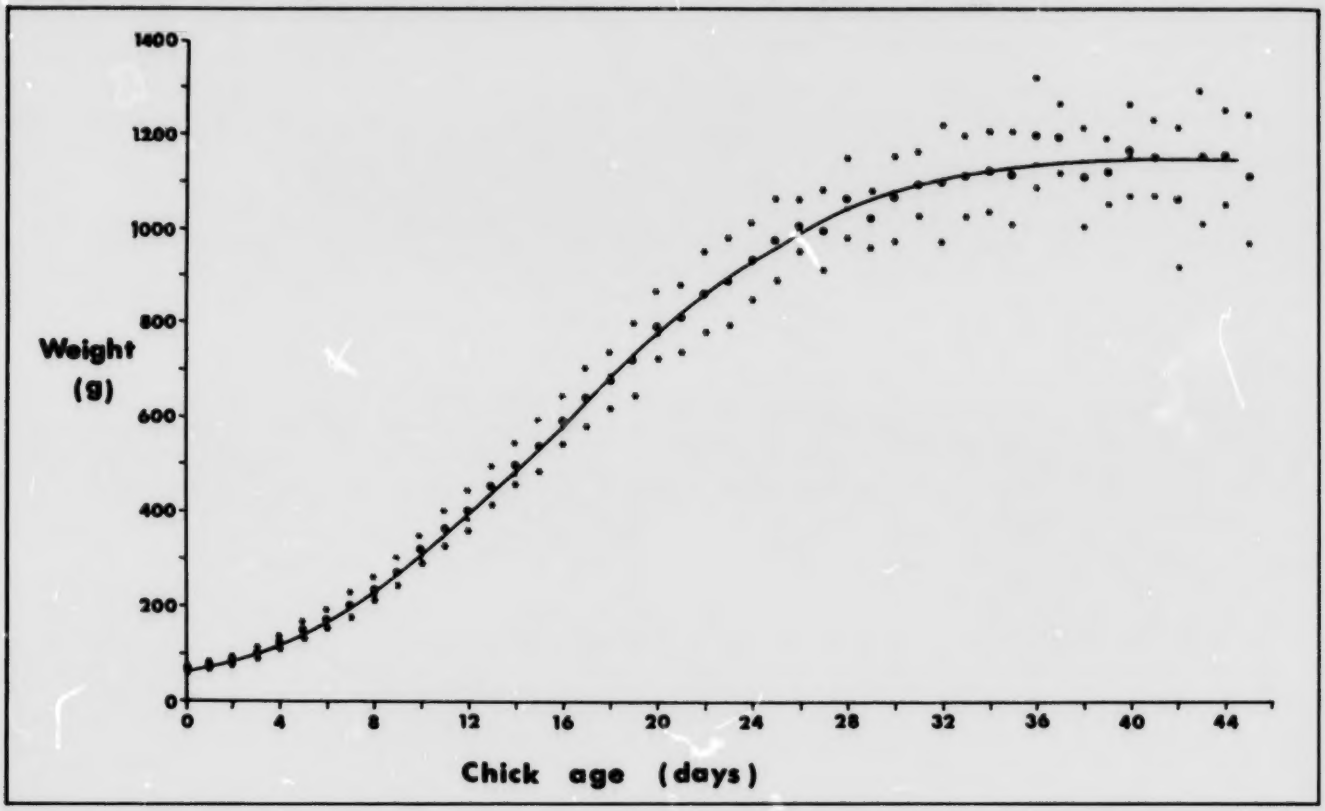


Figure 3
Weights of adult Skuas on Foula through the breeding season: breeding birds solid squares, non-breeders open squares

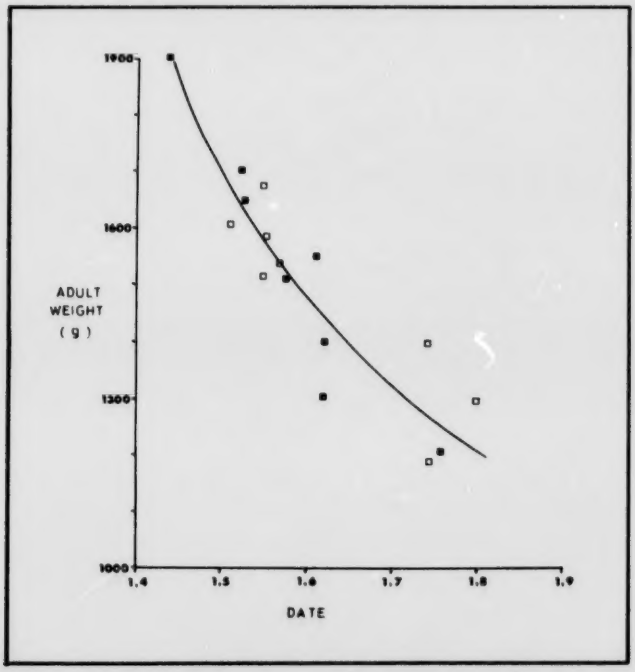
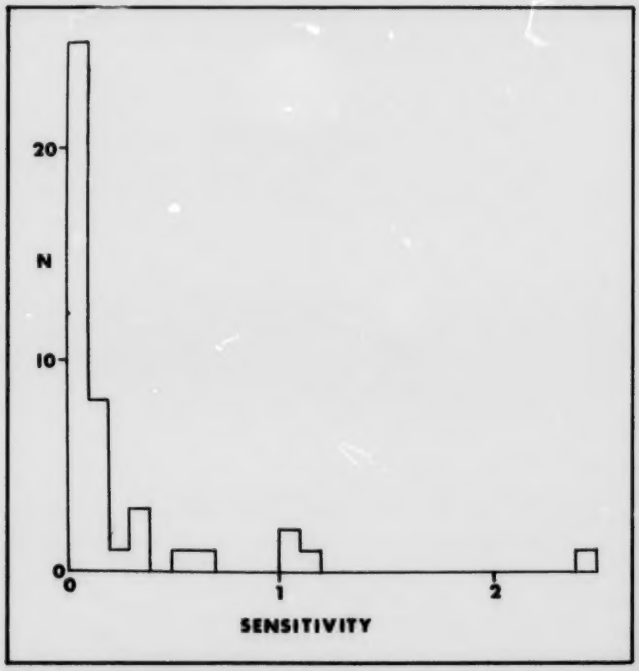


Figure 4
Model sensitivity (see text) to errors in the 44 parameters for Skua input data



plus or minus 30% of the mean (Furness and Cooper 1982). Further improvements in model precision are limited by the parameters population size, food utilization efficiency, and adult activity budget. As seabird populations can rarely be censused to an accuracy better than plus or minus 20% (Harris 1976) it is pointless to attempt to refine the model further unless the aim is to examine seasonal patterns of energy expenditure or the proportions used in different activities or by different parts of the population.

Adult existence requirements are equal to, and often much greater than requirements for foraging activity (Table 1). In Shetland, energy requirements of chicks or non-breeders are very small in comparison to the requirements of the breeding adults, even around the middle of the breeding season when numbers of non-breeders at the islands reach a maximum and chick food requirements peak (Fig. 6). The same pattern was found in a study of the energy requirements of seabird populations in South Africa (Furness and Cooper 1982). Adult existence accounted for 50–70% of the total population annual energy requirement, while the costs of moult and egg production represented less than 3% for each species (Table 2).

4.2.3. *Direct field measurements of metabolism* — Direct field measurements of food consumption or individual metabolism can be made using a number of recently developed and sophisticated techniques, but none of these has yet been applied to seabirds. Injection of radioisotopes of elements whose excretion rate is correlated with the rate of metabolism, injection of doubly labelled water (D_2O^{18}), and heart-rate biotelemetry all have potential (Furness 1982). Development of these techniques would provide a useful direct measurement of seabird population energetics, which could be used to validate the much simpler and cheaper use of bioenergetics models.

4.3. Conclusions from bioenergetics modelling

Further research into the activity budgets of seabirds will be necessary to improve the accuracy of bioenergetics models. Further research is also essential in order to determine the foraging ranges of seabirds from breeding colonies. Population energy requirements can only be set in context if the diets and foraging ranges of the seabirds are also known and there are data on the production of fish stocks within the foraging areas of the birds. Knowledge of seabird diets is often poor, and information on seabird foraging ranges is particularly limited.

Wiens and Scott (1975) estimated that the seabirds of coastal Oregon consumed 22% of the annual fish production. Furness (1978) estimated that the seabirds of Foula, Shetland, consumed about 29% of the fish production within a 45-km radius of the colony, and Furness and Cooper (1982) estimated that the seabirds of the southern Benguela system in the mid 1970s consumed 20% of the pelagic fish biomass. Seabird predation is clearly quantitatively important in some marine ecosystems and may potentially compete with fishing interests. The increases in

Figure 5
Model sensitivity for Arctic Tern input parameters

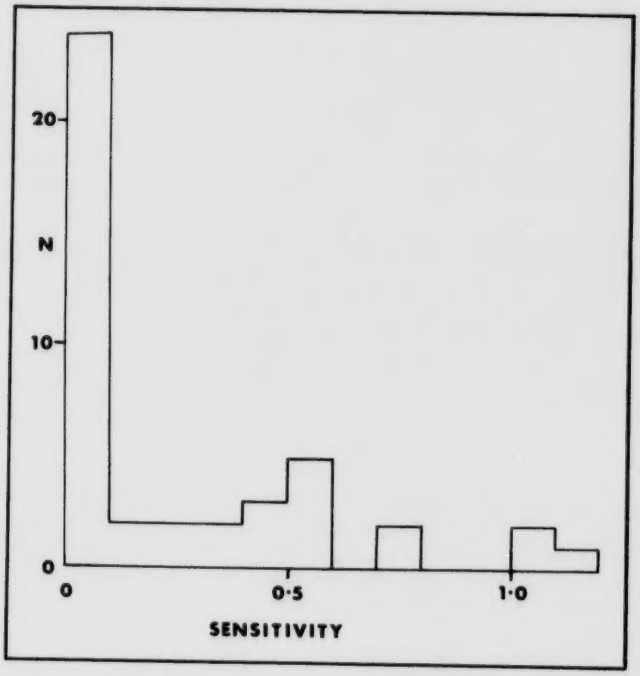


Table 1
Energy budgets of seabird populations estimated from bioenergetics modelling: Skua and Arctic Tern populations at a Shetland colony during the breeding season alone (from Furness 1978)

		Skua		Arctic Tern	
Population component	Energy allocation	Expenditure, million kcals/yr*	% of budget, breeding season	Expenditure, million kcals/yr	% of budget, breeding season
Breeders	existence	188.1	60.0	45.6	40.6
	activity	67.7	21.6	51.8	46.2
	egg production	1.2	0.4	0.5	0.4
	total	257.0	82.0	97.9	87.2
Non-breeders	existence	21.4	6.8	2.0	1.8
	activity	5.6	1.8	2.2	2.0
	total	27.0	8.6	4.2	3.8
Chicks	existence	21.1	6.7	8.4	7.5
	growth	8.4	2.7	1.7	1.5
	total	29.5	9.4	10.1	9.0
Population	total	313.5	100.0	112.2	100.0

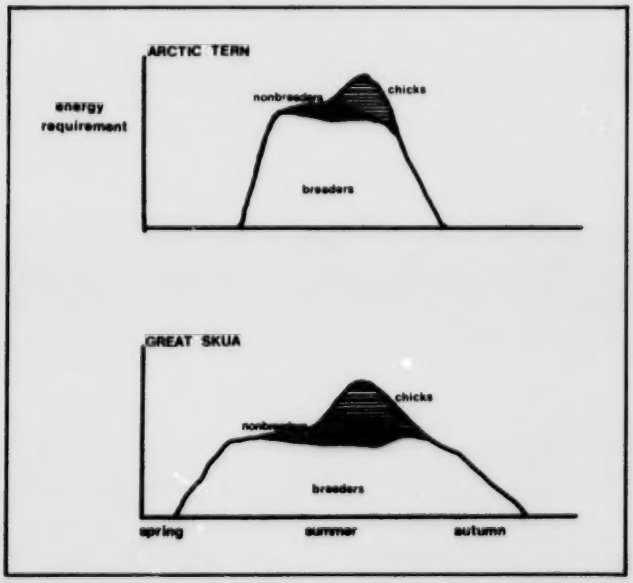
*1 kcal = 4.19 kJ.

seabird populations in Scotland (Furness, this volume), decreases of seabirds in southern Africa (Burger and Cooper, this volume), increases of seabirds and seals in the Antarctic (Croxall and Prince 1979), decreases of guano birds in Peru (Santander 1980), and breeding failure of alcids in the west of Norway (Lid 1981) can all be attributed to major switches in composition of fish stocks in these areas. Although the high predation rates of these seabirds help to explain their rapid response to changes in the marine ecosystem, it is not possible to make predictions about the changes in seabird population sizes from bioenergetics models alone. Consideration also has to be given to inter-specific relationships and effects of food shortage or excess on different aspects of population biology. No satisfactory models of these relationships have yet been constructed, but they are a logical sequel to bioenergetics modelling in order to gain further insight into relationships between seabird populations and fish stocks. For the remainder of this paper I shall consider the ways in which seabird populations are influenced by changes in food availability.

Table 2
Energy budgets of seabird populations estimated from bioenergetics modelling: seabirds in the southern Benguela system (from Furness and Cooper 1982). Energy expenditure in kJ × 10^8/year

	Jackass Penguin		Cape Gannet		Cape Cormorant	
Energy allocation	**Expen-diture**	**% of budget**	**Expen-diture**	**% of budget**	**Expen-diture**	**% of budget**
Adult existence	229.4	71.4	101.9	50.7	72.1	63.6
Adult foraging	62.4	19.4	72.7	36.1	32.3	28.5
Chicks	24.6	7.6	22.2	11.0	6.2	5.4
Adult moult	4.9	1.5	4.3	2.1	2.8	2.5
Egg production	0.4	0.1	0.1	0.1	0.05	0.0
Population total	321.7	100	201.2	100	113.4	100

Figure 6
Seasonal patterns in the energy requirements, while resident at the colony, of breeding, non-breeding, and young Skuas and Arctic Terns at Foula, Shetland, as estimated by bioenergetics modelling. The spring increases and autumn decreases are due to the arrival and departure of birds at the colony



5. Effects of food shortage on seabird communities

5.1. Mechanisms

Food shortage can influence seabird population dynamics by reducing breeding success or increasing adult mortality or delaying age of first breeding, or a combination of these. Seabirds are generally long-lived, and few studies have accurately measured their adult survival rates, let alone annual variations in survival rates or variations in survival related to colony size, population density, or food availability. Coulson and Wooller (1976) showed that the annual survival rate of adult breeding Black-legged Kittiwakes (*Rissa tridactyla*) fell as the study colony increased in size and density, and they associated this change with increasing competition, particularly for nest sites in the larger colony. Ollason and Dunnet (1983) have shown that annual changes in numbers of Northern Fulmars (*Fulmarus glacialis*) nesting on a small island in Orkney depend mainly on year-to-year variations in recruitment rate, which appears to correlate with food availability. Adult survival rate has shown little variation and does not correlate with changes in breeding numbers.

A consequence of culling Herring Gulls (*Larus argentatus*) has been a reduction in the age of first breeding (Chabrzyk and Coulson 1976, Duncan 1978). Nesting of younger birds is presumably possible due to reduced competition, although the relative roles of social behaviour and increased food per bird are unclear. The hormonal basis of such release is described by Carrick and Murray (1964), who implicate food reserves as the trigger for maturation.

Many studies have indicated that food availability is one of the main determinants of breeding success in seabird populations. Harris and Hislop (1978) showed that Atlantic Puffins (*Fratercula arctica*) select larger fish and species of high calorific value to feed chicks. Chick growth and fledging weights were highest when the diet consisted mainly of sprats (*Sprattus sprattus*), whereas in years when young whiting (*Merlangus merlangus*) were fed to chicks their growth was poorer. Food quantity and quality tended to be better at the Isle of May than at St. Kilda. Rates of increase of the two colonies parallel these differences in food availability, although there is little evidence that variations in fledging weight resulting from food shortage alter Altantic Puffin survival or subsequent return to the colony (Harris 1982).

Food availability to chicks may also influence breeding success in an indirect way. Atlantic Puffin breeding success is greater on sloping habitat than on flat habitat on Great Island, Newfoundland, as a result of the interaction between food availability and gull interference. Hungry chicks spend more time at the burrow entrance, exposing themselves to a higher risk of gull predation. Frequency of chick feeding was lower on flat habitat because gulls were able to kleptoparasitize food-carrying adults more successfully there, so that chicks on the flat habitat were more likely to suffer food shortage (Nettleship 1972). The complicated interaction between habitat, food availability, and the interspecific relations indicates the difficulty of relating seabird community dynamics to food supplies.

Brood-size-reduction is a strategy employed by a number of seabird species. This is clearly correlated with food availability, and optimizes fledgling production in relation to food supply (Hahn 1981). Procter (1975) showed that the older chick in broods of the South Polar Skua

(*Catharacta maccormicki*) would attack and kill the younger if deprived of food for a period of time. Young (1963) found that it was exceptional for the younger chick to survive to fledging when food was in short supply. The closely related Skua in the North Atlantic regularly rears both chicks to fledging. The population is currently growing rapidly under favourable conditions provided by the whitefish industry and increased sandlance stocks (Furness and Hislop 1981) so that chicks even in supernormal broods rarely go short of food. Haymes and Morris (1977) found that Herring Gulls at Lake Erie were able to rear supernormal broods without increased brood reduction or predation because they were able to make use of human-supplied artificial food sources in addition to their natural food supply, while Hunt (1972) found that chicks fed on garbage and fish waste grew faster than those in more isolated colonies where only natural foods were available. Hunt and Hunt (1976) found that Glaucous-winged Gull (*Larus glaucescens*) chick survival correlated closely with growth rate and both were determined largely by food availability.

Thus, several studies have shown the importance of food availability, directly or indirectly, in determining breeding success. Modelling seabird population responses to changes in fish stocks would require a theoretical framework allowing relationships between food availability and breeding success, as well as adult survival rate and age of first breeding, to be quantified. I know of only one such model at present. Using a combination of central place foraging theory (Hamilton and Watt 1970, Orians and Pearson 1979) and a deterministic simulation model of Common Murre feeding rate and chick growth, Ford *et al.* (1982) concluded that the breeding success of a Common Murre population would fall steeply with a food density reduction of only 10–30%, and a reduction of food availability of 40% or more would lead to total reproductive failure. Overfishing of fish stocks can easily lead to a stock density reduction of this magnitude (Hempel 1978) so that serious effects on seabird population dynamics could be expected.

Our lack of data on the relationships between food availability and adult survival rate or age of recruitment preclude similar modelling of these aspects of population dynamics. Further studies of the relative roles of breeding success, recruitment, and adult survival on seabird population change are required before reliable models of population dynamics can be constructed. In addition, influences of interspecific effects need to be taken into account, which will prove even more difficult to incorporate into a simulation model.

5.2. Examples of the influences of food availability on seabird populations

Having discussed the need to construct models to investigate the influences of changing fish stocks on seabird communities, and the problems in measuring effects of food availability on parameters of population dynamics, I shall finish by describing a few documented examples of fishery–seabird interactions.

Lid (1981) has reviewed the history of alcid breeding success and population change in west Norway over the last 25 years. He showed that Atlantic Puffins, Common Murres, and Razorbills (*Alca torda*) have not decreased noticeably in numbers during this period, but since 1969 all species have shown dramatically reduced breeding success compared with earlier years, while average weights of adult Atlantic Puffins also seem to have decreased. Lid (1981) attributes these changes to the reduction in Norwegian spring-spawning herring (*Clupea harengus*) stocks from 10 million metric tons in 1958 to 0.5 million metric tons by 1969, as a result of overfishing. At the same time the catches of sandlance in Norwegian waters have grown from less than 10 000 t in the 1960s to 150 000 t by the end of the 1970s. These two species were the main prey of the alcids in the 1960s and their disappearance from the diet seems to be the cause of the alcids' recent breeding failures. The model proposed by Ford *et al.* (1982) would predict total breeding failure with this scale of reduction in food availability.

Similar relationships can be seen particularly well in the Benguela ecosystem, where seabird numbers can be estimated from historical records of guano yields and census counts (Crawford and Shelton 1978; Burger and Cooper, this volume). Of particular interest is the differential response of the three main groups of seabirds. Cape Gannets (*Sula capensis*) are strong fliers and travel considerable distances from breeding colonies in search of food. Cormorants (*Phalacrocorax* spp.) have wettable plumage and are weak in flight so their range is rather smaller. Jackass Penguins (*Spheniscus demersus*) are flightless and travel short distances from their colonies to feed. Intense exploitation of pilchards (*Sardinops ocellata*) and the larger age classes of pelagic species in general (Crawford 1981), has reduced food availability to these seabirds. Cape Gannets have been able to exploit waste from demersal trawlers working far offshore and increase their foraging range to exploit distant fish shoals, but Jackass Penguins have been unable significantly to alter their foraging ranges or diets. As a result, Jackass Penguins have shown a much greater population decline than have Cape Gannets (Burger and Cooper, this volume). A similar differential effect of food shortage has been noted in Peru, where the Guanay Cormorant (*Phalacrocorax bougainvillii*) has suffered much higher mortality rates and population decrease than the Peruvian Booby (*Sula variegata*) as a result of the reduction of anchovy (*Engraulis ringens*) stocks (Jordan and Fuentes 1966, Nelson 1978, Santander 1980). In this case too, the broader ecological niche of the booby probably gave it an advantage when food became short.

Pearson (1968) showed that the proportion of available time spent in foraging decreased with increasing body size in the seabird community on the Farne Islands, Northumberland. If this rule is generally applicable then the smallest species are likely to be most severely affected by food shortage as they have little opportunity to increase their foraging effort. Similarly, dominance hierarchies at feeding sites behind whitefish trawlers may result in some species suffering a disproportionate reduction in food supply when availability decreases (Furness and Hislop 1981).

6. Conclusions

Bioenergetics modelling provides useful quantitative assessments of the impact of seabird communities on fish stocks and suggests the likelihood of changes in fishery practices or fish-stock sizes affecting seabird numbers. However, it is not clear which aspects of population biology would be altered by food shortage, or what interactions would take place between seabird species. Simple predictions would be that species with specialized feeding methods and a high dependence on the food that has been

reduced in availability would be likely to decline in numbers. Species with restricted foraging ranges, low in the feeding status hierarchy, or of small size are particularly at risk. It is to be hoped that focusing of attention on this complex subject will lead to the development of more sophisticated predictive models and the monitoring of seabird population biology in areas where fisheries are particularly intense.

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Brown Pelicans and the anchovy fishery off southern California

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1. Abstract

Prey-species-diversity for seabirds such as Brown Pelicans (*Pelecanus occidentalis californicus*) is low in the Southern California Bight (SCB). Breeding success and winter populations of Brown Pelicans increase or decrease with increases or decreases in the dominant prey, northern anchovy (*Engraulis mordax*). Availability of anchovies is usually related to their abundance. SCB seabirds could be affected by intensive commercial fishing activities, as has been documented in other areas, such as Peru, South Africa, and northern California. Three viewpoints usually complicate conservation attitudes toward seabird–fishery interactions: (1) they may be viewed as negative competitive impacts by humans on seabirds with resultant population declines of an aesthetic resource; (2) they may be viewed as negative competitive impacts by seabirds on resources of value to people, with economic implications that perhaps call for intentional control of seabirds; and (3) seabirds may be viewed as practical indicators of general environmental "health" or as indicator species of some specific utility in resource management. In the SCB, negative effects of commercial anchovy fishing on Brown Pelican populations remain a potential threat rather than a reality, but fishing impact has been recently suggested by low pelican reproductive rates and breeding population declines at one breeding colony close to an intensive fishery in Mexico. Previous to 1979 both pelican reproduction and fishery catches appeared to fluctuate in relation to anchovy abundance levels. After 1979, despite large increases in anchovy harvest quotas, catches in the US were far below the quota limits. Had quotas been reached, we would have anticipated negative impacts on pelicans and other seabirds on a wider scale in the SCB. To minimize such impacts, we suggest that fishing restrictions at low levels of anchovy abundance will be more effective than restrictions at high levels. Seabird populations would probably be least affected by fishing regulations that avoid prolonged low fish abundance.

2. Résumé

La diversité des espèces de proies disponibles pour certains oiseaux de mer comme le Pélican brun (*Pelecanus occidentalis californicus*) est plutôt faible dans la baie du sud de la Californie (B.S.C.). Le succès de la reproduction et les populations hivernales de Pélicans bruns augmentent ou diminuent selon les fluctuations de leur proie principale, soit l'anchois du Pacifique (*Engraulis mordax*). La disponibilité des anchois est généralement reliée à l'abondance des pélicans au point que la pêche commerciale intensive pourrait nuire aux oiseaux de mer de la B.S.C. comme cela s'est déjà produit dans d'autres régions comme le Pérou, l'Afrique du Sud et le nord de la Californie. Trois points de vue différents sur les interactions «oiseaux de mer–pêche» viennent généralement faire obstacle aux efforts de conservation : 1) ces interactions peuvent être considérées comme une intervention concurrentielle négative de l'homme sur les oiseaux de mer avec les déclins de population d'une précieuse ressource qui en découlent; 2) elles peuvent être considérées comme une intervention concurrentielle négative des oiseaux de mer sur certaines ressources utiles à l'homme avec ses répercussions économiques et peut-être aussi les intentions de lutte contre les oiseaux de mer qui s'ensuivent; et 3) les oiseaux de mer peuvent être considérés comme des indicateurs pratiques de «l'état de santé» général de l'environnement ou comme des espèces indicatrices d'une certaine utilité dans l'aménagement des ressources. Dans la B.S.C., les effets négatifs de la pêche commerciale aux anchois sur la population de Pélicans bruns demeurent une menace potentielle plutôt qu'une réalité, mais l'incidence de la pêche a récemment été évoquée par les faibles taux de reproduction du pélican et le déclin des effectifs à une colonie de reproduction située près d'une zone de pêche intensive au Mexique. Avant 1979, la reproduction du pélican et les prises de poissons ont semblé fluctuer selon l'abondance des anchois. Après 1979, malgré l'accroissement considérable des contingents de pêche aux anchois, les prises ont été de beaucoup inférieures aux limites de contingentement aux États-Unis. Si les contingents avaient été atteints, nous aurions pu prévoir des retombées négatives à plus grande échelle sur les populations de pélicans et d'autres oiseaux de mer dans la B.S.C. Pour réduire au minimum ce genre de répercussions, nous supposons que les restrictions de pêche imposées lorsque les disponibilités d'anchois sont plutôt faibles seront plus efficaces que celles décrétées lorsqu'elles sont abondantes. Les populations d'oiseaux de mer seraient probablement moins touchées par des règlements de pêche ayant pour objet de prévenir les périodes prolongées de pénurie des stocks de poissons.

3. Introduction

Several studies on marine birds (reviewed by Ashmole 1971) emphasize food supply as a major factor regulating their populations. This idea has been logically extended by conservationists who ask the question: do intensive (or unrestricted) commercial harvests of important prey species affect marine bird population levels? This leads to another question: how much can an important prey species be harvested without undesirable effects on marine

bird populations? And, finally, what compromises must people and birds make in managed ecosystems?

There are several well-known examples of severe population declines of marine birds in settings of intensive, yield-oriented commercial fishery programs: Peru (Paulik 1971, Idyll 1973, Tovar 1978, Glantz 1979), South Africa (Crawford and Shelton 1978), and perhaps northern California (see Ainley and Lewis 1974). Furness (1978) has modelled a seabird–fish system, and warns of possible detrimental effects of intensive commercial fisheries. Nettleship (1977), Brown (1980) and Ainley (1980) have also urged managers of marine resources to give greater consideration to marine birds as components of marine ecosystems, especially where fisheries and seabirds might interact. This is a concern shared by most marine ornithologists. There are some attempts being made to provide a "forage reserve" within fishery management plans to maintain adequate population levels of prey species for consumers other than people (see Pacific Fisheries Management Council [PFMC] 1978, MacCall 1980, Gress and Anderson 1982).

The Southern California Bight ("SCB" is defined by the Southern California Coastal Water Research Project 1973) provides an opportunity to study fishery–seabird interaction. One can question whether increased harvests of northern anchovy (*Engraulis mordax*) in the SCB would be compatible with present or larger pelican populations. A knowledge of the ecology of the California Brown Pelican (*Pelecanus occidentalis californicus*) breeding in the SCB may provide insight, and management efforts to provide self-sustaining, natural populations of SCB seabirds may benefit from an understanding of pelicans. Attitudes in our society towards interactions between birds and people depend on how abundant seabirds are, the prevailing philosophy of resource use, economic priorities, and which of those views predominate.

Our objectives here will be (1) to review research on Brown Pelicans in the SCB to show the relationships of food supply to changes of certain population measurements (size, breeding performance, survival rates) and compare the related responses of commercial fishing and pelican population parameters to changing anchovy abundance, and (2) to suggest some premises for seabird management based on the data currently available.

4. Responses of birds and the fishery to anchovy changes in the SCB

Anderson *et al.* (1980) have initially examined relationships between anchovies, the fishery, and pelicans. Our discussion here is based mostly on that and subsequent reports (Anderson *et al.* 1982, Anderson and Gress 1983). The SCB may be somewhat unusual in that its diversity of prey for seabirds is reduced over that originally present (see Anderson *et al.* 1982). Pacific sardines (*Sardinops sagax*) along the California and Baja California coast were overfished and became virtually non-existent by the 1950s (see Radovich 1981). Ainley and Lewis (1974) speculated that the failures of some seabird species (e.g. *Phalacrocorax auritus*) along the northern California coast have been due primarily to the lack of sardines. Anchovies have largely replaced sardines as a prey item of Brown Pelicans south of Point Conception (see Anderson and Anderson 1976 and MacCall, this volume), and at present are almost completely dependent on anchovies as a food source during the breeding season in the SCB (Kelly *et al.* 1981). Pelicans and commercial fisheries in the SCB are also presently taking the same stock and same age-classes of anchovies (Sunada *et al.* 1981). This situation differs from that reported by Randall *et al.* (1981) in South Africa where Jackass Penguins (*Spheniscus demersus*) were found to have consumed a younger age-class of cephalopod than that taken by the fisheries.

In comparing food supply or abundance of a resource to performance by birds or the fishery, many measurements of success can be used, each with perhaps a different biological meaning. Anchovy abundance measurements correlate best with pelican reproductive success on a localized basis that relates, in turn, to young-rearing strategies and colony location (see Anderson *et al.* 1982). Other measurements might relate better to the fishery.

Commercial anchovy harvests are regulated (see PFMC 1978) and should vary according to the total biomass of harvestable resource in the SCB, and this is our basis of comparison here (Fig. 1). Birds and the fishery probably do not respond exactly to the same aspects or segments of a "shared" resource (but see Sunada *et al.* 1981 for the SCB), but for lack of more appropriate measures, we use this common basis. The relationship between this wide-scale measurement of food for pelicans (i.e. area-wide anchovy abundance in the SCB) and abundance of pelicans (Anderson *et al.* 1980) is weaker than that between local food abundance and number of birds. Yet, local levels of food probably often relate to regional levels, because large-scale events are also important influences on the availability of food to seabirds over large geographical areas (see Boersma 1978).

Anderson *et al.* (1980, 1982) have shown that at moderate to high anchovy abundance levels in the SCB, pelican reproductive rates (but not numbers of breeding pairs at the breeding colonies) are correlated with abundance (Fig. 1, but see original references for details). Similar relationships are also believed to exist for other species of seabirds in the SCB such as Western Gulls (*Larus occidentalis*) and Xantus' Murrelets (*Endomychura hypoleuca*) (see Hunt and Butler 1980). The question of mortality and food relationships is now under study, but Anderson and Gress (1983) believe that pelicans are typical seabirds in that mortality rates are more constant than reproductive rates.

Changes in winter populations (when censuses would record mostly resident pelicans) from year to year in the SCB are also related to changes in anchovy abundance in the preceding breeding season (Fig. 2). The pelican population changes shown in Figure 2 were determined from Christmas bird count indices; these are the only long-term data available, but they are believed to be reliable (see Anderson and Anderson 1976). For purposes of our discussion here, we will assume that pelican population status is closely related to food supply, but due to ecological circumstances the relationship is not totally linear. In the SCB, this food supply is highly variable in amount (MacCall 1980). Since it is not diverse, any changes in population of a dominant species (such as the northern anchovy) will have the potential to cause variation in seabird populations, as suggested by MacCall (this volume).

US commercial anchovy catches, at least through 1980, appear to have responded generally to changes in SCB biomass of anchovies (Fig. 3 *vs.* Fig. 1). Prior to 1978, catch responses seem only weakly related at best to the catch quotas established each year by the California Fish and Game Commission (Fig. 3). The Northern Anchovy Fishery

Management Plan, (PFMC 1978), developed according to the Fisheries Conservation and Management Act of 1976, has allowed larger US quotas than previously (Fig. 3).

A complicating and perhaps overriding factor in the fish/person/pelican interrelationship in the SCB is the increasing harvest of anchovies by the Mexican commercial fishery along the northwest Baja California coast. This fishery harvests a large proportion of the same subpopulation of anchovies regulated more conservatively in the US (Fig. 3). In Mexican waters, catches have exceeded those in the US since 1979 (see Mais 1979), largely because the fishery there is unrestricted (Fig. 3); it is a fishery that has probably increased independently of anchovy abundance. Interestingly, signs of deterioration of Brown Pelican reproductive success and breeding populations at the Los Coronados Islands (part of the SCB pelican population, see Anderson and Gress 1983) began in 1979 and continued at least through 1982 (D.W.A. and F.G., field notes). The commercial fishery in Mexico might have significantly reduced productivity and numbers of pelicans and other seabirds dependent on anchovies for the first time in our 14 years of study. That conclusion remains speculative, however, owing to the absence of data showing a precise "cause and effect" relationship.

The drop in US catch (despite increased quotas) has been largely due to economic factors (high cost of fuel, increased processing costs, lack of demand for fish-meal, and increased quotas for the more lucrative Pacific mackeral, *Scomber japonicus*; A.D. MacCall, pers. comm.). Quotas are also more complex than shown in Figure 3; for example, the 1980–81 formula was subdivided as follows: 163 000 t total harvest quota by formula, of which 151 000 was for reduction or fish-meal purposes, and of this amount only about 73 000 was allowed by the California Fish and Game Commission for onshore reduction (Stauffer and Picquelle 1981). There is doubt, however, that this final restriction functionally limited the fishery; we cite the example only to illustrate how complex a quota can be.

Recent US catches of SCB anchovies (1978–80) have also contained relatively more young fish. Mais (1981) warns that a "failure" of two age-classes (such as has occurred in the past) could further depress anchovy populations to

Figure 1
Patterns of anchovy use by pelicans and the fishery in the SCB. A. Variations in anchovy biomass estimates (in km^2 of school surface) and pelican productivity (fledging rates). Anchovy abundance estimates to 1979 are after Mais (1974) and Anderson *et al.* (1982). From 1979 on, biomass estimates are from Stauffer (1980), Stauffer and Parker (1980), and Stauffer and Picquelle (1981), and they are converted to equivalent units based on 1978 comparisons. B. Changes in harvest of anchovies by the US fishery from 1971 through 1980 expressed in metric tons $\times 10^3$ (from Mais 1981). C. Relationship of SCB overall estimates of anchovy abundance (using same units as above) and pelican fledging rates. The curve was fitted by eye. Regional comparisons like this are more imprecise than local ones but they are presented here because they can be directly applied to management units of the anchovy fishery. The "x" represents an anomalous year (1972–73) (see further explanations in Anderson *et al.* 1980, 1982, and Anderson and Gress 1983)

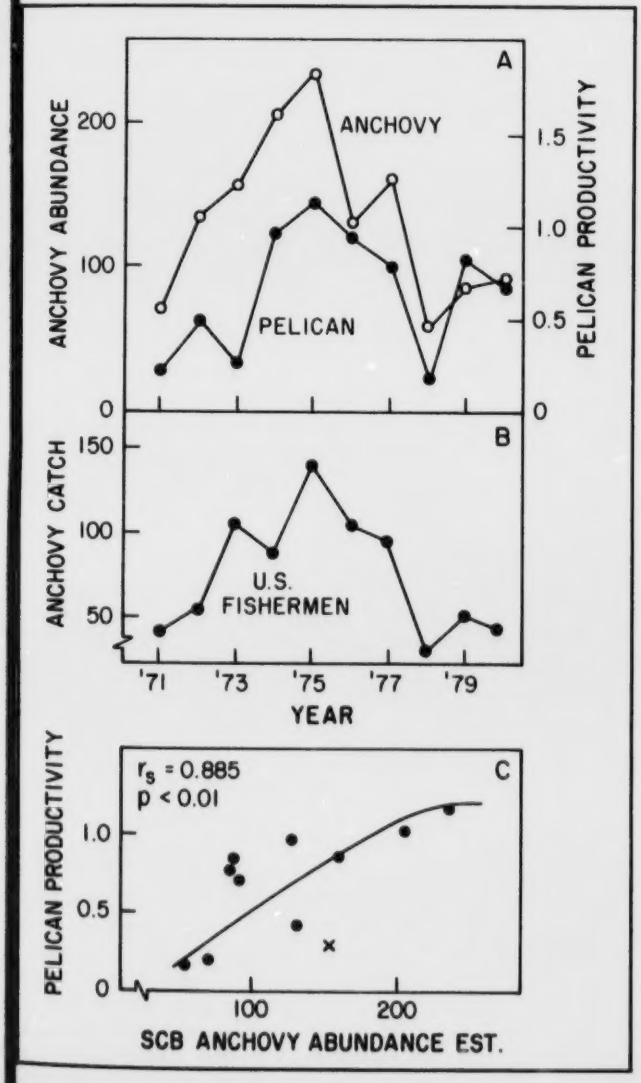
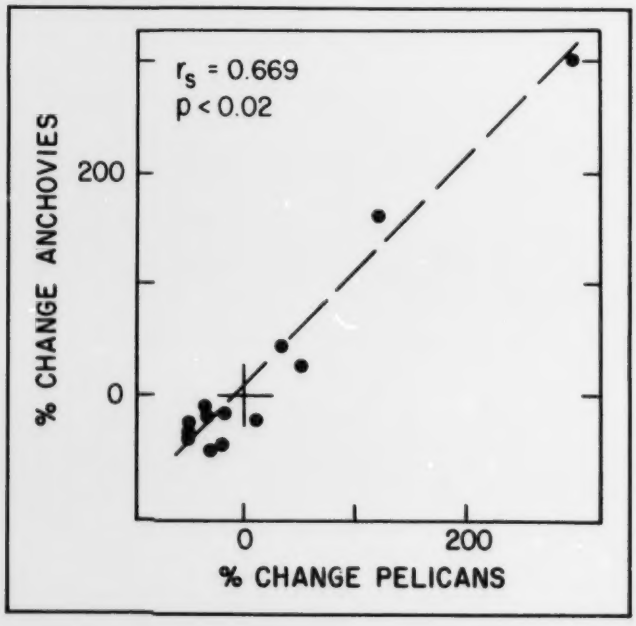


Figure 2
Relationship between annual percentage changes in Brown Pelican population indices (from Anderson and Anderson 1976) and annual percentage changes in anchovy abundance (from various sources, see Anderson and Anderson 1976), 1957 to 1970. Due to DDT, pelican population indices from 1971 to 1973 were too consistently low to measure changes (see Anderson *et al.* 1975)



"undesirably low levels." Before they were commercially exploited, anchovies were very scarce at times (MacCall 1980, this volume). Intensive fisheries might increase the frequency of this occurring. We conclude from data obtained prior to 1979 that fisheries in the past had no measurable negative effect on Brown Pelican reproductive success or population. Although potential problems are becoming evident in the SCB's southern (i.e. Los Coronados Islands) Brown Pelican breeding population, US quotas to date seem to have had minimal influence on actual catch, which has responded to availability, and also to market and economic fluctuations.

5. Responses of Brown Pelicans and other species to food

Nelson (1977, 1978, 1979) believes that populations of most tropical and subtropical seabirds are regulated by density-independent phenomena related to variations in food supply. DeMaster (1981) uses the term "resource-dependent" to describe some marine mammal populations, and makes the following claims:

> . . . that many marine mammal populations are probably resource-dependent; that density dependence is a special, and perhaps unusual, case of resource-dependence; that the availability of resources is a function of both density and environmental conditions; that resource-limited populations can decline more rapidly than increase; and that some resource-limited populations are more likely to be found increasing than decreasing or remaining stable.

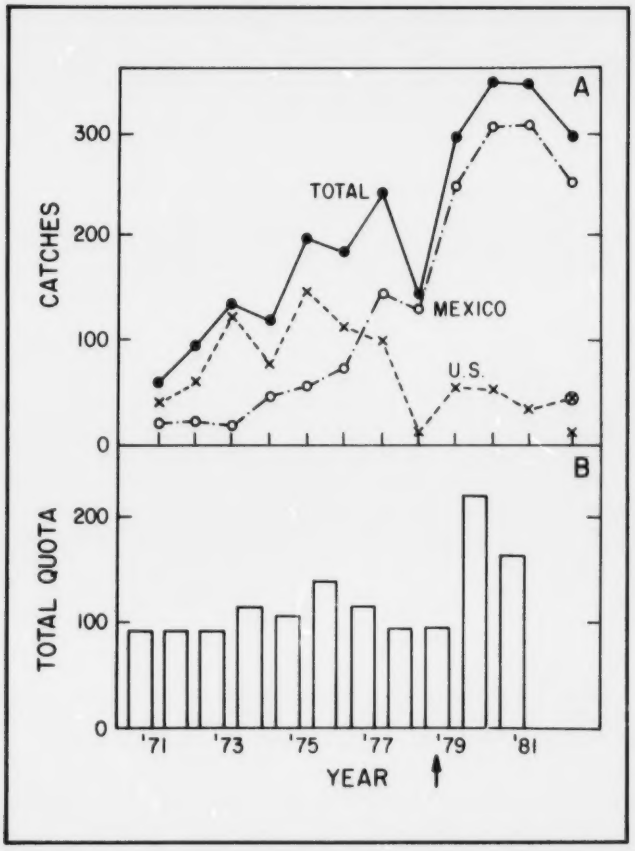
Eberhart (1977) and Estes (1979) in referring to marine mammals have similar suggestions. Marine mammals, however, may differ from Brown Pelicans in that their reproductive rates may be less flexible, since they are usually limited physiologically to one young, which is seldom abandoned. Also, pelicans probably have little or no regulating effect on their food supplies (Anderson *et al.* 1980); this is probably true for all SCB seabirds (MacCall, this volume). All natural predation on adult anchovies may not even have an important effect in regulating SCB anchovy spawning biomass (PFMC 1978) because of the great and dominant variation in environmental conditions of the SCB (MacCall 1980, this volume).

In comparison to marine mammals, pelicans and other seabirds probably have reproductive rates that are more responsive to environmental factors that affect the food supply. This may be the primary population response in seabirds, and one that is more important than compensatory changes in juvenile mortality as in many marine mammals (see Eberhart 1977). Data on Brown Pelicans from the Gulf of California (D.W. Anderson, unpubl.) suggest that juvenile mortality rates are more strongly related to date of hatch and colony synchrony within a given year. Our observations relating to pelicans in the SCB suggest that relationships between food supply and population parameters are similar between pelicans and resource-dependent marine mammals, but that the birds may have more flexibility in responses to food through more variable reproductive rates, and less flexibility in their ability to "integrate" their food supply over time through extensive energy reserves.

Boersma (1978) has shown that the breeding pattern of Galapagos Penguins (*Spheniscus mendiculus*) is closely related to oceanographic conditions (via food availability); she suggested a similar adaptation in Brown Pelicans (*P. o. urinator*) of the same area. In the Peruvian coastal ecosystem, Brown Pelicans (*P. o. thagus*) respond to food shortages with "massive adult mortality and nest desertion" (Duffy 1980). Food-related mortality in adult California Brown Pelicans is very rarely observed (D.W. Anderson, unpubl. data). *P. o. thagus* apparently responds differently to food shortages (which are often extreme) when compared to seabirds in other ecosystems (Duffy 1980); yet high and rapidly responsive reproductive rates are necessarily emphasized in the reproductive strategies of both *P. o. thagus* and *californicus*. SCB Brown Pelicans should logically illustrate a pattern intermediate between *thagus* and more "typical seabirds" because of less extreme shifts between what Horn (1978) terms "profligate breeding and dogged survival."

Brown Pelican reproduction in the SCB populations can also be termed "resource-limited." Food, as an ultimate factor in affecting reproductive rates, is a major source of variation even in the situation of chronic pollution (Keith 1978, Anderson and Gress 1983). One could argue that if

Figure 3
Anchovy catches (A) and various US fishery quotas (B) off southern California. Catches are from Mais (1974) and R. Klingbeil (pers. comm.). Quotas are from Kaneen (1977), Stauffer and Parker (1980), Stauffer (1980), and Stauffer and Picquelle (1981). Values for 1981–82 were projected; the circled "x" represents projected catches and uncircled "x" represents actual catch about half-way through the season. The arrow indicates the beginning of the US management plan (PFMC 1978), which has a Mexican fishery component as part of the recommended quota. Mexican fisheries are not subject to quota restrictions



reproduction were food-limited and straightforwardly related to food (provided also that no catastrophic events intervene), individual pairs would always attain maximum potential reproduction until they began to affect (deplete) their food supply, with density-dependent competition occurring, or reproduction levelling off as physiological limits were reached. However, we view prey location and capture as a probabilistic process. Pelicans do not go to a "food trough," but rather have a variable probability of detecting mobile prey, depending ultimately on prey abundance and behaviour (availability). Thus, mean prey abundance and/or availability will have some relationship to mean reproductive success for the breeding unit or colony that utilizes this shared food source.

Numbers of Brown Pelicans breeding in the SCB have increased in recent years from the pollution-caused depletions of the early 1970s (Anderson and Gress 1983). Their reproductive rates have continued to reflect the abundance of their prey and their population levels may have done so as well (see previous discussion), irrespective of population level at the time of change in food abundance. With a highly variable carrying capacity (for seabirds reflected through highly variable food supplies), such as is observed in the SCB, pelican numbers should also fluctuate greatly once population recovery from pollution-related catastrophies (see Anderson *et al.* 1975) is complete. However, the variation should also be dampened by the responsive reproductive rates discussed and the tendency for mortality rates to remain stable that is characteristic of most seabirds (see Anderson *et al.* 1982). The fact that pelican populations are serially correlated from one year to the next (see Anderson and Anderson 19' 6) would tend to further dampen fluctuations that are related to resource-dependent changes in reproduction. As predicted for marine mammals by DeMaster (1981), pelicans might also be in a state of increase more often than decrease. Thus, ideally, we could view the population response of the SCB pelicans in the manner suggested by MacCall (this volume) and Anderson *et al.* (1980) for Brown Pelicans *per se* (Fig. 4): only at the very high and very low populations should one observe clear density-dependence among adults. The usual situation should be that of "phase B" (Fig. 4).

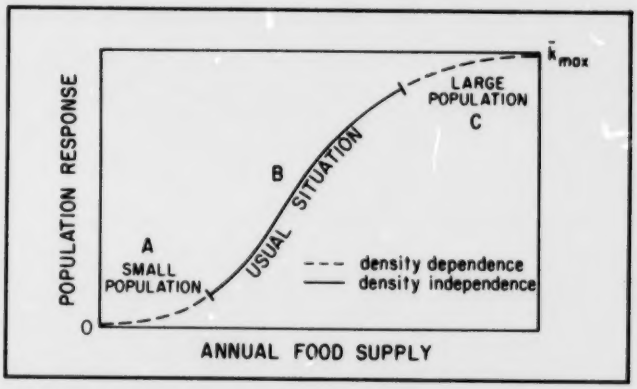
As already seen, pelicans respond to biomass of prey (indirectly through availability) but only to a small geographic proportion of it (Anderson *et al.* 1980). The birds require a much larger prey population size than that actually consumed to produce availability levels in which an adequate ration can be obtained by individual pelicans in the breeding population. One could therefore logically argue that decreases in mean, long-term abundance of the prey base could alter pelican population levels and perhaps even slow or hinder the present recovery of the SCB Brown Pelicans (Anderson and Gress 1983).

6. Conservation awareness toward seabirds

Human attitudes toward familiar seabird species (such as the Brown Pelicans) and subsequent conservation policies are probably influenced by population levels of the birds. Typical human attitudes might vary in relation to the seabird population levels depicted in Figure 4, with the following effects on management policy:

1. At very low levels (A in Fig. 4), density-dependence could become important through lack of such necessities as social stimulation of breeding (see Gochfeld

Figure 4
Idealized short-term seabird population responses (at various initial population levels) to varying levels of food supply. This should not be confused with the logistic growth model



1980), lack of co-operative food finding or, in extreme cases, through the unusual genetic effects in small populations (See Frankel and Soulé 1981). At this stage, primary conservation strategy becomes one of preserving genetic diversity. Management of food resources is likely to have relatively less effect than, say, selective breeding, colony protection, artificial feeding, and so on. By this time it might be too late for effective natural population management, in any case.

2. In the linear phase of this idealized response (B in Fig. 4), the target species' population response is probably density-independent, which is typical of the real situation for most population levels most of the time. This situation most commonly involves actions by resource managers. A catastrophic loss of food supplies could suddenly shift the population into density-dependent competition, or other natural or unnatural catastrophies could suddenly reduce populations. In these rare but, given enough time, almost certain instances of catastrophy, about all wildlife managers can do is regroup and reformulate new management policies. Most of the time, however, populations would be expected to remain in the linear range of response, so a management policy based on it should be effective.

Also in the linear range of response (B in Fig. 4), application of the "indicator species" concept has been suggested (Nettleship 1977, Siegfried and Crawford 1978, Ainley 1980, Brown 1980, Anderson and Gress 1981, and others). Sunada *et al.* (1981) have gone so far as to term the California Brown Pelican "a sampling instrument." During our studies, the Brown Pelican has been an "obligate specialist" feeding on a limited-diversity prey base in the SCB. In the Bering Sea, only about 7% of the seabird species are true "specialists" (Ainley and Sanger 1979). Species with limited diets can be useful indicator species if they have only a small or negligible effect on the abundance of their prey. Breeding Brown Pelicans only consume, maximally, an estimated 0.08% of total anchovy spawning biomass (Anderson *et al.* 1980).

A weak relationship between reproductive success of California Brown Pelicans at the two major breeding colonies and overall mean anchovy estimates suggests that pelican reproduction also depends on regional SCB phenomena, particularly oceanographic events. We expect reproductive rates to be a sensitive indicator of *local* food conditions for pelicans, as has been proposed for other species (see Dorward 1962, Lack 1966:267).

Pelicans may also prove to be indicators of changing environmental conditions, just as other seabirds appear to be in areas off South America affected by large-scale oceanographic events (Murphy 1936, Jordan and Fuentes 1966, Boersma 1978, Duffy 1980). The general relationships seen may provide a way to monitor food abundance (see Anderson *et al.* 1980). Indicator species, no matter what the circumstances that predispose them to qualify, should be ones that respond most rapidly to changes or perturbations for a variety of reasons: ecological, physiological, circumstantial, and so on. Our experiences suggest that the Brown Pelican is such an indicator in the SCB, but whether it would have the same utility under a heavy fishing regime is not known. Once the value of an indicator species is recognized, a paradox arises: the species merits a large degree of protection for its useful qualities, but in order to indicate a deteriorated resource the indicator species itself must deteriorate.

3. Once populations reach a level where environmental factors cause individuals in the population to interfere or compete, another density-dependent phase would occur (C in Fig. 4). Here, conservation may no longer be the issue and "predator control" might be considered. Intentional control of seabirds has never been an issue in the SCB, but unfortunately in other areas predator control is often considered at lower population levels. Such considerations of control and the risks that might be involved are well illustrated by a quote from a report of the Instituto del Mar del Peru (1981):

> It must be kept in mind that the assumed product values [fish meal *vs.* guano] are probably fixed in favor of meal but, far more important, this approach to the matter ignores the threat it presents to the very existence of a bird population that has already reached perilously low levels. Also, the ecological consequences of eliminating the bird populations are not understood. In other animal populations, control of predators has failed to give the expected increase in the prey species, for example, because predation takes more of the diseased individuals, and in their absence disease increases. Until more is known about the interactions between the bird and anchoveta populations, any type of predator control program to reduce the birds would be extremely hazardous.

7. Bird–fishery responses compared

Anderson *et al.* (1980) have discussed the relationship between pelican reproductive rates and anchovy fishery catch (idealized here in Fig. 5) and suggest three possible biological explanations:

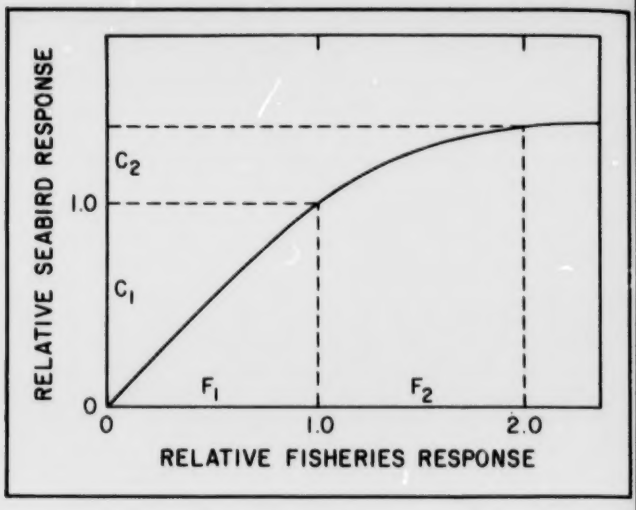
1. Both predators are limited by their own asymptotic rates, but birds approach their limit much sooner.

2. The two predators respond to different aspects of fish behaviour that differentially change with fish abundance.

3. There may be direct competition between the fishery and birds, with the fishery being the controlling or more effective competitor (this is the least likely explanation due to the low level of fishing pressure).

If both consumers (the fishery and pelicans) have responded to biomass in the past in an uncompetitive way (pelicans through physical–physiological constraints and the fishery through biomass-oriented regulations and economic

Figure 5
Idealized fishery and seabird responses compared. The curve is based on data taken from Anderson *et al.* (1980) with responses converted to equal units for comparisons. "F" represents the proportional fishing response and "C" the proportional seabird response



profitability, as previously discussed), their relationships might tell us at what point significant person–bird competition might occur. And if pelicans are indicators of environmental condition, then perhaps other seabirds that depend on similar food resources may respond similarly.

We do not interpret Fig. 5 causally, and if birds and the fishery have been responding independently, then restrictions on fishing would have an indirect rather than a direct effect on seabirds. The ratio of pelican to fishery response crudely measures interaction potential: a higher value should indicate a greater differential reaction. From previous discussion (Fig. 4) and by examining the generalized response (Fig. 5), we anticipate that pelicans are most sensitive to variations in food in the linear phase of their response to changing food supplies. In that phase, enhancement of the forage base (such as through fishing restrictions) should be most effective because the ratio of C1:F1 is maximal. Whereas, at higher anchovy biomasses (assuming still that the fishery is biomass-responsive, such as through regulations), (C1 + C2)/(F1 + F2) is about 0.7, and the marginal response C2:F2 is about 0.4. From the viewpoint of seabird conservation in a fishery that is based on a biomass response, a progressive restriction of fishing effort at the lower biomasses, together with fishing closures below a minimum level established as a "forage reserve" (see PFMC 1978), seems potentially most beneficial to seabirds. It follows that larger harvests at higher biomasses should have less effects on seabirds, unless *direct* competition between the fishery and the birds occurs.

Natural changes in species composition of the prey base of Brown Pelicans and other seabirds in the SCB would lead to different year-to-year interrelationships. This would necessitate responsive management and long-term monitoring of seabirds and their prey.

8. General discussion

Depressions of seabird populations caused by commercial fisheries in systems biologically and oceanographically both similar and dissimilar to the SCB (see MacCall, this volume) were mostly characterized by depressed natality that apparently could not balance mortality related to density-independent phenomena. In fact, it seems likely that seabird species that are resource-limited and long-lived rely on variations in natality (and perhaps also on variations in juvenile mortality) for population regulation. In a highly variable environment, as suggested by DeMaster (1981), such populations would usually be in an increasing phase and dependent on sufficient recruitment to maintain this phase. Thus, severe interactions with a commercial fishery are likely to lead to population depression (MacCall, this volume).

The SCB situation remains encouraging mostly because of the relatively inactive state of the anchovy fishery. We urge continued monitoring of the situation to detect changes in the future. Unusual events such as those off Peru reported by Tovar (1978) and Glantz and Thompson (1981), are known also to occur (but less intensely) in the SCB and nearby areas (Radovich 1961, Anderson 1973). Such natural events which deplete the food supply of resource-limited species of seabirds may have resulted in the evolution of high survival rates and resource-responsive reproductive rates, such as those we observe in Brown Pelicans.

Recovery of the SCB Brown Pelican population from the acute effects of DDT-contamination was more rapid than expected, although it is not as yet complete (see Anderson *et al.* 1975, 1977; Anderson and Gress 1983). The recovery might have been even more rapid were it not for chronic eggshell thinning. Rapid recovery was perhaps due in part to the propensity for such species to recover from reduced population levels mostly through improvements in reproductive rates (Anderson and Gress 1983) once the perturbations were lessened or removed. The rapid recovery certainly attests to the resiliency of seabird populations such as the Brown Pelican.

Managers in the SCB now have a tool for the protection of seabird food resources: the Anchovy Fishery Management Plan and Endangered Species Act (see Gress and Anderson 1982). However politicians can directly decide the actual level of interaction between pelicans and the fishery that will be allowed. Perhaps when more precise natural history data are available, we will be able to anticipate the results of various management options. Recently, new techniques have been developed to better estimate actual biomass of SCB anchovies (Parker 1980). We have used previous anchovy biomass estimates as population indices and measured relative changes. We hope that eventually accurate conversions will be developed to enable better recommendations as to allowable levels of fishing.

For the present, we urge continued monitoring of fish, bird, and other wildlife populations, as well as monitoring of environmental parameters in sensitive areas. For seabirds in particular, conservation involves both the colony (see Anderson and Keith 1980) and habitat at sea. The potential for depression of seabird populations in the SCB through large commercial harvests of anchovies is still a reality in our opinion. Fortunately, resource-limited species such as pelicans seem to be resilient to environmental change.

9. Acknowledgements

We thank A.D. MacCall, D.N. Nettleship, and an anonymous reviewer for criticisms and comment. Our studies were supported by a number of agencies listed in our individual papers cited here.

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Seabird–fishery trophic interactions in eastern Pacific boundary currents: California and Peru

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1. Abstract

The nature of seabird–fishery trophic interactions is investigated by comparative and simulation studies. Peru and California have very similar fish communities, but the seabird communities are less similar. The relationship between seabirds and fisheries cannot be considered outside the context of natural patterns of forage availability. The forage base is characterized by extreme variability, serial correlation over years, geographic expansion and contraction with changes in abundance, and species replacement events. El Niño presents special reproductive and survival problems to Peruvian seabirds. Seabird impact on fish abundance may have been significant in Peru, but is probably small in California. Fisheries may reduce food availability to seabirds with subsequent decrease in reproductive success. A simulation model suggests that a variable food supply results in variable seabird abundance. Fisheries may reduce food to levels below those necessary to sustain seabird populations, but patterns of decline may easily be misinterpreted due to long trends of population increase and decrease.

2. Résumé

L'auteur examine la nature des interactions trophiques existant entre les oiseaux de mer et la pêche par des études comparatives et simulées. Le Pérou et la Californie comptent des communautés de poissons très voisines, ce qui n'est pas le cas pour celles des oiseaux de mer. Il est impossible d'étudier le rapport entre les oiseaux de mer et la pêche sans tenir compte des modes de distribution naturels et de la disponibilité de la nourriture. La source de nourriture se caractérise par une extrême variabilité, une corrélation périodique au fil des ans, une expansion et une contraction géographiques selon les fluctuations d'abondance et certains cas de remplacement d'espèces. Le courant El Niño pose des problèmes de reproduction et de survie spécialement chez les oiseaux de mer péruviens. La prédation des oiseaux de mer peut avoir eu un effet important sur l'abondance du poisson au Pérou, mais cet effet est probablement modeste en Californie. En revanche, la pêche peut réduire la disponibilité de nourriture pour les oiseaux de mer suivie d'une baisse de la réussite de la reproduction. L'application d'un modèle de simulation révèle qu'un approvisionnement de nourriture variable entraîne des fluctuations d'abondance chez les oiseaux de mer. La pêche peut réduire la disponibilité de nourriture à des niveaux inférieurs à ceux nécessaires pour soutenir les populations d'oiseaux de mer, mais les courbes de déclin des populations peuvent être facilement mal interprétées à cause des tendances à long terme d'augmentation et de baisse des populations.

3. Introduction

Fisheries can perturb trophic relationships in an ecosystem to an extent far exceeding the scope of conventional ecological experiments. However, interpretation of fishery effects is very difficult due to lack of replication or experimental control. Two methods of confronting these problems are comparative studies and simulation modelling. Comparison of fisheries and components of ecosystems may aid our understanding of those entities to the extent that they are similar, but the consequences of their differences must also be recognized. Simulation modelling is a complementary tool of great potential, especially if supported by a sound empirical basis of natural history. The model may grossly simplify fishery and ecosystem components, but the range of possibilities within that model can be fully explored by means of perfectly replicated and controlled "experiments." These two approaches are used here to examine seabird–fishery relationships in southern California and Peru.

3.1. Eastern boundary currents

Southern California is strongly influenced by the California Current, which is one of four similar ocean currents in the world. The other three of these "eastern boundary currents" are the Peru Current, the Canary Current, and the Benguela Current off southwest Africa. These currents are similar in many respects, both physical and biological. They represent the eastern limbs of major oceanic gyres, and are characterized by a wide and moderately slow equatorward flow. Characteristically, the nearshore regions of these currents are sites of coastal upwelling, whereby wind patterns combine with the effects of the earth's rotation to cause deep, cold, nutrient-rich water to be brought to the surface as large plumes. The upwelled water often supports high primary production of phytoplankton, with subsequent secondary production of zooplankton. These in turn support an abundance of higher predators such as fish and squid, and finally larger fishes, marine mammals, and seabirds. Useful reviews of eastern boundary current characteristics are given by Bakun and Parrish (1980), and Wooster and Reid (1963). The California Current has been the most thoroughly studied example,

and is reviewed by Hickey (1979) and by Reid *et al.* (1958). Upwelling itself is the subject of a recent symposium edited by Richards (1981).

3.2. Species assemblages

Eastern boundary currents are characterized by remarkably consistent assemblages of pelagic fishes (Table 1). As pointed out by Bakun and Parrish (1980), this similarity suggests that the environmental processes which determine the reproductive success of these fishes are similar as well. Except for the hake (*Merluccius* spp.) and in some cases the larger jack mackerel (*Trachurus* spp.), all of the fishes in Table 1 tend to be the object of surface fisheries utilizing purse-seine technology. The collapse of the fishery for each of these surface fishes has occurred in at least one of the four current systems (see Clark 1977, Murphy 1977, Newman and Crawford 1980, Troadec *et al.* 1980, Radovich 1981). The reason for these collapses has tended to be excessive growth of fishing capacity combined with extreme natural variability of the resource. The latter subject will be discussed in the following section.

The assemblages of guano-producing seabirds breeding in eastern boundary current areas also tend to be similar, although not as similar as assemblages of fishes. Seabirds are particularly influenced by the quality of breeding sites, which may explain the paucity of species breeding in the Canary Current. The assemblages in the two areas in the southern hemisphere bear the greatest similarity, in that they share penguins and sulids (boobies and gannets). The California Current lacks these two groups, but features a large assemblage of alcids (auks, puffins, murres, guillemots) which closely parallel the penguins in many respects (Storer 1960). Pelicans are abundant off California and Peru, but the species residing off South Africa seems to have affinity for freshwater fishes rather than for coastal pelagic fishes (Burger and Cooper, this volume). Cormorants are perhaps the quintessential guano bird, the name itself being associated with the Guanay Cormorant (*Phalacrocorax bougainvillei*) of Peru. Although the dominant cormorants off Peru and South Africa feed mainly on pelagic fishes, those off California feed more on fishes associated with the bottom (Ainley *et al.* 1981). In addition to the species listed in Table 1, gulls and terns (Laridae), shearwaters (Procellariidae), and storm petrels (Hydrobatidae) commonly are associated with eastern boundary currents, as well as many other coastal habitats. Although seabirds would seem to be more geographically mobile than fishes, the fish assemblages are more consistent among the eastern boundary current systems.

The preceding discussion has purposefully excluded offshore archipelagoes. The Canary Islands and the Galapagos Islands are similarly situated at offshore and equatorward ends of their respective currents. Both are rich in tropical and open-ocean seabirds, but are not likely to be impacted by coastal pelagic fisheries due to their relative isolation from the mainland.

Table 1
Comparison of pelagic fish species in three major eastern boundary currents (from Bakun and Parrish 1980)

	California	Peru	South Africa
Anchovy	*Engraulis mordax*	*E. ringens*	*E. capensis*
Sardine	*Sardinops sagax*	*S. sagax*	*S. ocellatus*
Jack mackerel	*Trachurus symmetricus*	*T. symmetricus*	*T. trachurus*
True mackerel	*Scomber japonicus*	*S. japonicus*	*S. japonicus*
Bonito	*Sarda chiliensis*	*S. chiliensis*	*S. sarda*
Hake	*Merluccius productus*	*M. gayi*	*M. capensis*

4. The forage base

The remainder of this paper will focus on Peru and southern California. In these systems only the anchovy is small enough to be a universal forage item for seabirds. However, younger individuals of the other surface species appear in seabird diets, and of course larger seabirds can consume larger prey. Clupeoids (anchovy and sardine) are the dominant forage items, and the following discussion will treat the variability of these species as well as their interrelationships.

4.1. Temporal variability

The northern anchovy (*Engraulis mordax*) off California has been monitored closely since 1950 by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) even though a substantial commercial fishery for it did not develop until the mid 1960s. The dynamics of the stock have been sufficiently studied so that satisfactory population models have been developed (Huppert *et al.* 1980, MacCall 1980*a*). The anchovy stock has shown large fluctuations in the 30 years it has been monitored by CalCOFI, but the nature of its probable variability is better demonstrated by a time segment from a long-term simulation model (Fig. 1).

The anchovy simulation model is described by Huppert *et al.* (1980). Simulated "actual" abundances are generated by random variability about the historical stock–stock relationship of CalCOFI anchovy abundance estimates. Simulated "observed" abundances include another random variable representing relative measurement error. The simulation includes effects of fishery harvest, which is governed by a quota of one-third of the excess over one million metric tons "observed" biomass.

Two properties of this time-series are especially important. The first property is extreme variability in abundance: simulated biomass varies over a 30-fold range from smallest to largest values in this segment of the simulation. Actual estimates of anchovy abundance off California increased 30-fold from 1952 to 1965 (MacCall 1980*a*), suggesting that the simulation model may even be conservative in its variability. MacCall showed the long-term variability of anchovy abundance by means of probability distributions (Fig. 2), which suggest that abundance is approximately log-normally distributed over time.

The second property of anchovy abundance is its year-to-year serial correlation. Huppert *et al.* (1980) examined the serial-correlation properties of the simulation model, and found sequential biomasses to have a correlation coefficient (r) of about 0.6. Abundant years tend to be followed by abundant years and scarce years tend to be followed by scarce years. Approximately 40% (r^2) of the variance in abundance can be explained by the previous year's abundance, and indeed this is very near the annual survival rate of anchovy biomass, which is about 45% (MacCall 1980*a*).

The Peruvian anchoveta (*Engraulis ringens*) also appears to be quite variable in abundance, but the extent of that variability is not clear. The anchoveta sustained adult biomasses of 10–25 million metric tons despite intense harvesting during the 1960s. However, after the collapse of

the resource in the early 1970s, biomasses have fluctuated between 2.5 and 6 million metric tons under greatly reduced fishing pressure (Tsukayama and Alvarez 1980, 1981).

Sardine (*Sardinops sagax*) stocks in Peru and California also appear to be volatile. MacCall (1979) showed recruitment in the California sardine to be highly variable, serially correlated, and to show little compensatory *per capita* increase at depressed stock sizes. Sardines in Peru increased from negligible abundances during the decade of the anchoveta fishery to a large fishery in the early 1980s.

4.2. Geographic variability

As Murphy (1977) points out, clupeoid fish stocks typically expand and contract with changes in abundance. For example, the range of the northern anchovy off California, as indicated by the occurrence of larvae, expanded from 1952 to 1965 (Fig. 3). As a result of this expansion, the density of anchovies spawning in the nearshore region of southern California changed relatively little with respect to overall abundance. Similar patterns have been observed in Peru, where the anchoveta has contracted into local pockets along the coast, and sardines have expanded offshore (Santander 1980, 1981).

In view of the tendency of the forage base to expand and contract, location may be an important factor in productivity and stability of seabird colonies. Colonies located near the centre of the fish stock will tend to have a more constant food supply than will colonies located toward the periphery. Examples of this geographic aspect of seabird–fishery interactions are provided by the California sardine fishery, which contracted southward into southern California during the mid 1940s (Murphy 1966). Ainley and Lewis (1974) have speculated that the larger seabirds breeding at the Farallon Islands near San Francisco were severely impacted by the disappearance of sardines. Unfortunately, seabird activity at the Farallon Islands was not consistently

Figure 2
Long-term probability distributions for observed northern anchovy abundance under two levels of exploitation (from MacCall 1980*a*); I) Unfished; II) Quota of one-third of the observed adult biomass in excess of one million metric tons (*cf.* Fig. 1)

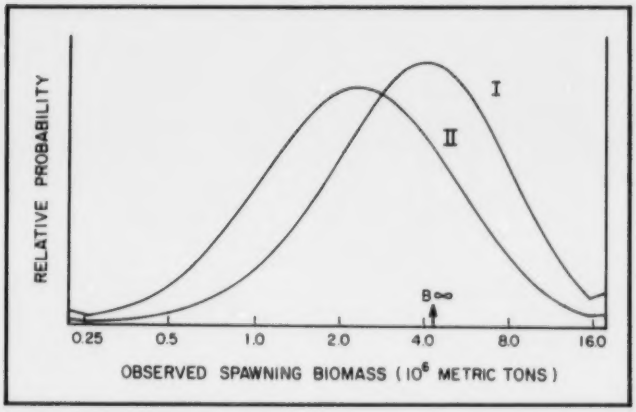


Figure 1
Simulated time series of "actual" and "observed" northern anchovy abundance (from Huppert *et al.* 1980). Dashed line is "observed" abundance below which fishery quota is zero. See text for details

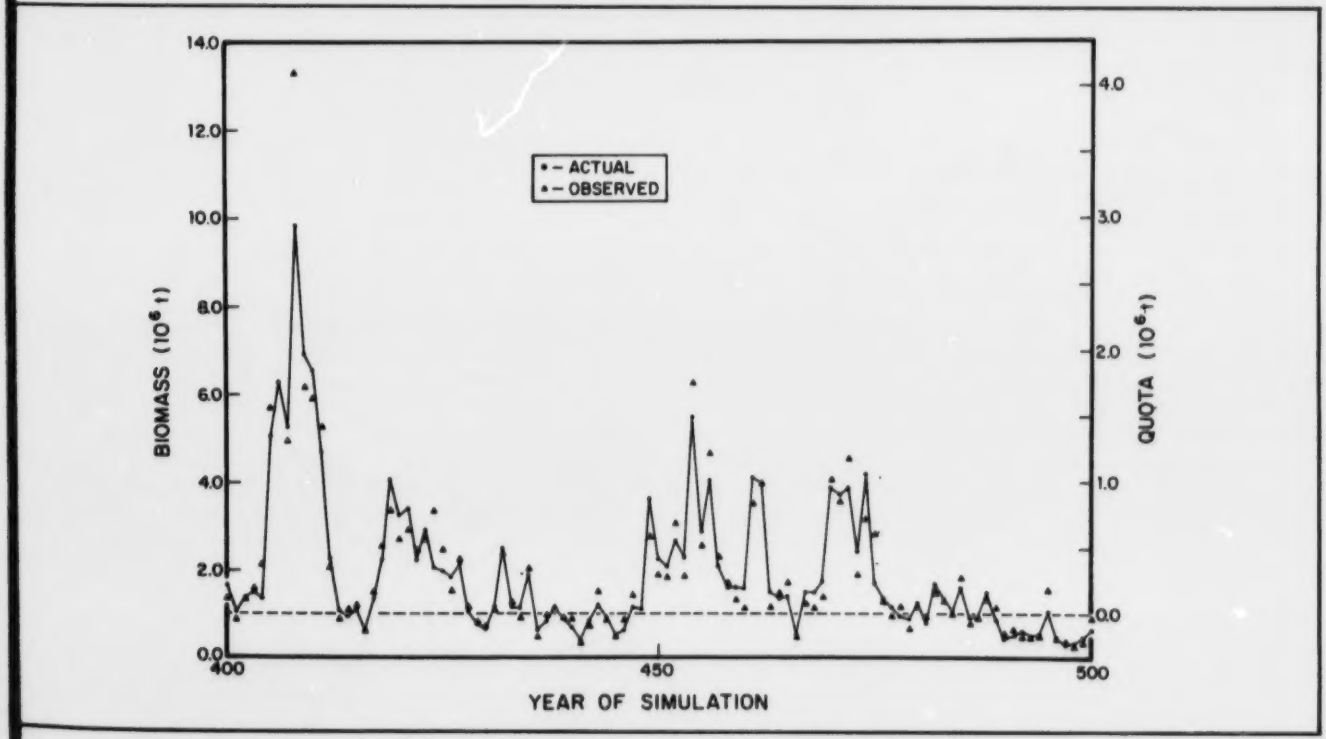
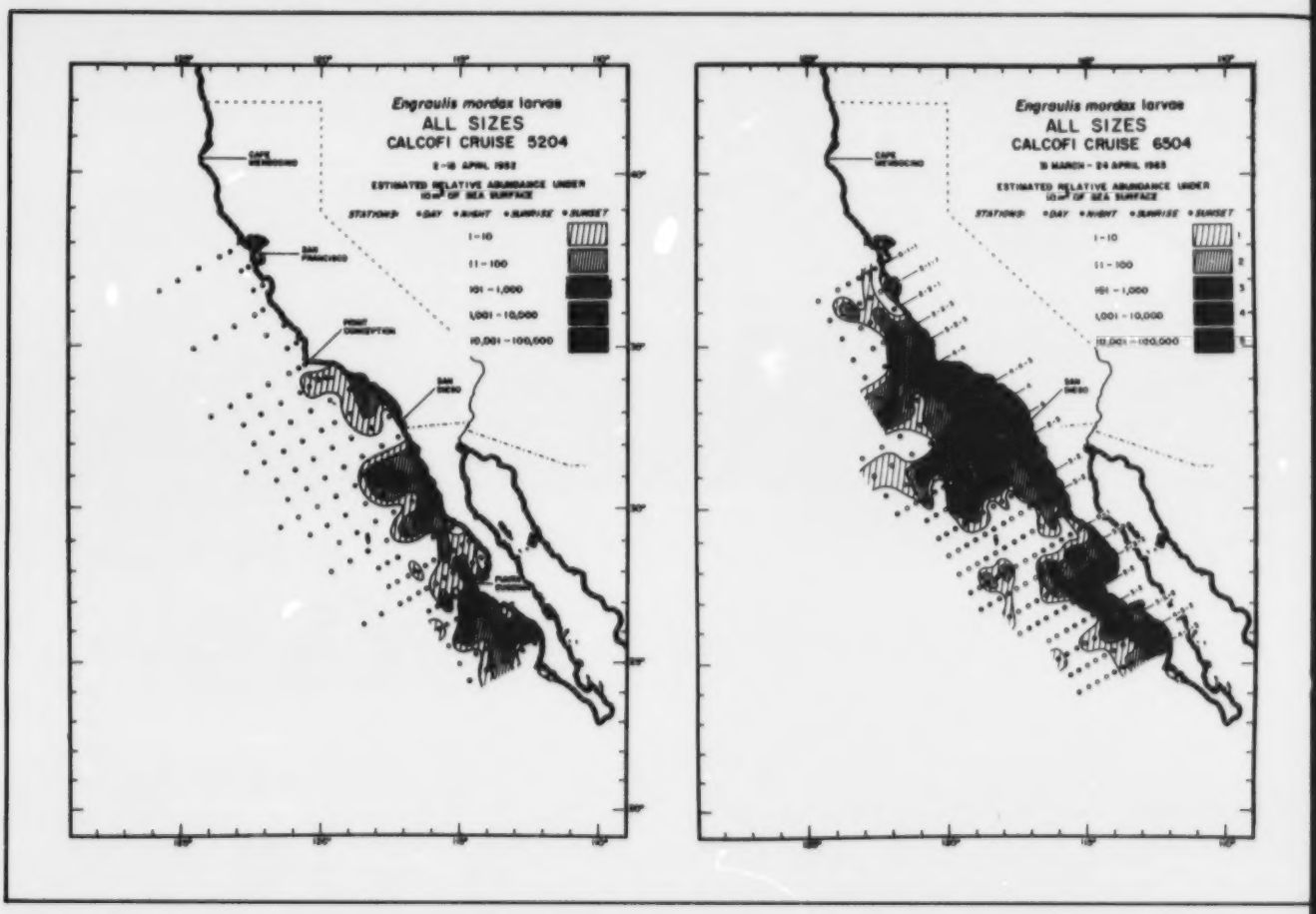


Figure 5
Geographic distribution and abundance of northern anchovy larvae at two levels of stock abundance (from Kramer and Ahlstrom 1968)



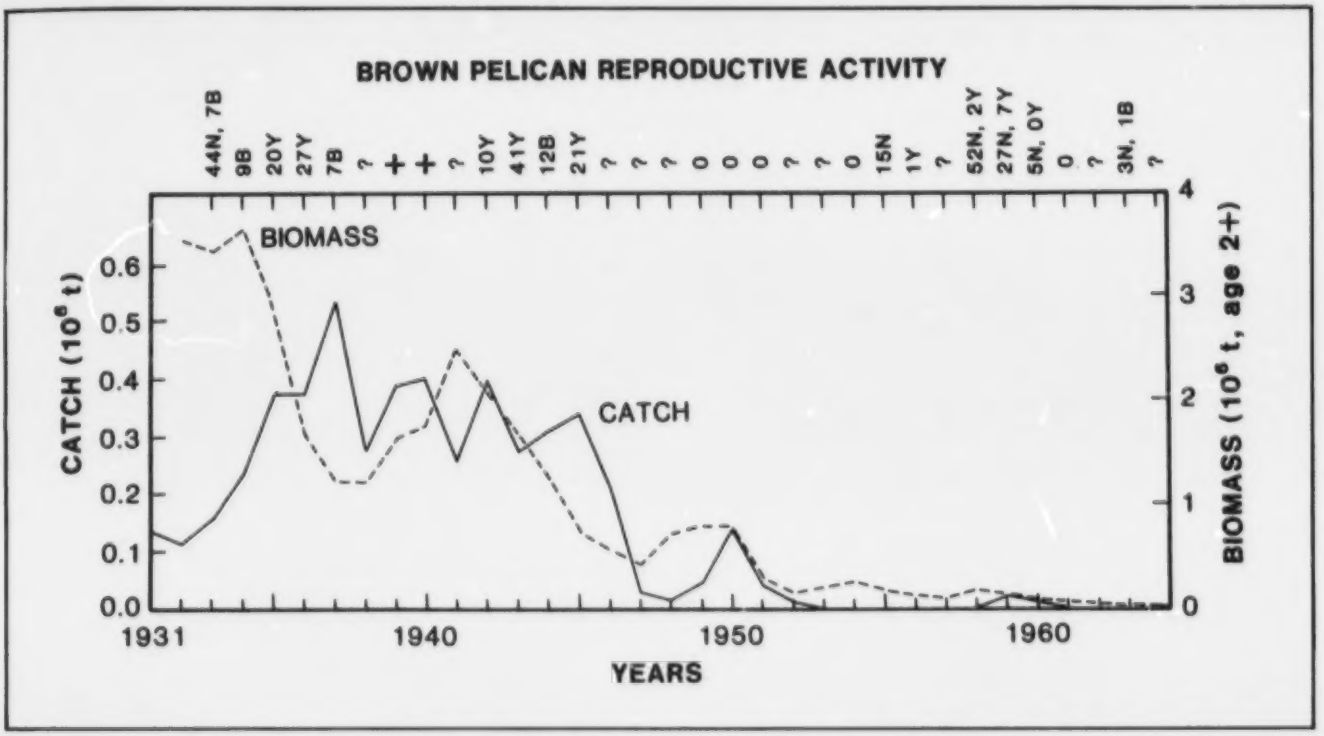
monitored until recently. A somewhat better case can be made for the Brown Pelican, (*Pelecanus occidentalis californicus*) which has sporadically nested at Point Lobos, near Monterey (Fig. 4). Baldridge (1973) has compiled a fairly continuous history of pelican breeding activity at that location since 1933. Pelican nesting activity, reproductive effort, and success roughly coincide with local sardine abundance as indicated by central California sardine fishery harvests. Although the sardine fishery continued for several years in southern California, the 1944–45 season was the last prosperous year for both the Monterey sardine fishery and the Point Lobos pelican colony. Notably, an extreme warming of the waters off California occurred during 1957–60, the so-called "warm water" period. The southern California sardine fishery briefly improved during these years, and many marine organisms extended their ranges northward (Radovich 1960, 1961). The pelican breeding attempts at Point Lobos during the late 1950s were probably associated with this warm period. The very poor success of the nesting activity was most likely due to the combination of DDT pesticide contamination (Anderson *et al.* 1975) and insufficient forage. Keith (1978) has shown that these two factors combine synergistically to severely reduce reproductive success.

4.3. Anchovy–sardine relationship

The decline of the California sardine population was followed by a large increase in anchovy abundance in southern California and to a lesser extent in central California. Murphy (1966) interpreted these trends as competitive replacement, and on the basis of goodness-of-fit, Silliman (1969) claimed to have used these data to substantiate the Lotka-Volterra competition theory. On the other hand, evidence of sardines and anchovy abundance from scale deposition rates in anaerobic sediments of a southern California basin indicated that the two species have varied similarly, rather than inversely, over the past 150 years (Soutar and Isaacs 1974). Reviews of the anchovy–sardine replacement hypothesis are given by Daan (1980) and MacCall (1980*a*).

The recent decline of anchoveta and increase of sardine in Peru has tended to strengthen the idea of replacement as a characteristic phenomenon among clupeoid fishes. Still, the mechanisms causing these changes have not been determined. Both anchovies and sardines are filter feeders, and cannibalism of their own eggs and larvae is probably the main density-dependent mechanism regulating their abundance (MacCall 1980*b*). If these two fishes

Figure 4
Brown Pelican reproductive activity at Point Lobos (Baldridge 1973) in relation to central California sardine catch (Murphy 1966) and total adult sardine biomass (Murphy 1966, MacCall 1979). Symbols: *N* = nests, *B* = broods, *Y* = young, + = some activity, 0 = no activity, ? = no observations made



inhabit the same area, they are certain to also be predators on each other's spawning products. Given the relatively low degree of compensation in the stock-recruitment relationships of these fishes, interspecific predation rather than competition is probably the mechanism governing their interaction. Such a mechanism would be expected to result in a relatively unstable relationship between the two fishes. Differential responses to exogenous influences such as environmental variability and selective fisheries may further destabilize the relationship.

Given the slow response time characteristic of anchovy–sardine replacement events, seabirds and other predators may not benefit from the relative stability usually attributed to a diverse forage base. However, the sedimentary scale record of Soutar and Isaacs (1974) suggests that maintenance of sardine–anchovy diversity may be a viable management objective. Sardine scales were present in all but one 5-year time segments in the 140 years up to 1950, but in only one segment in the 20 years following 1950. By reducing fishing pressure on either species when its abundance is low, fishery management should be able to maintain both species in at least moderate abundances, and by doing so, reduce the response time for replacement when conditions are favourable.

Anchovy–sardine replacement events have now occurred in both California and Peru. In both cases, the sardine-dominated system apparently has been centered poleward of the anchovy-dominated system. In California, the sardine fishery was largest in central California, and extended as far north as British Columbia (Murphy 1966), whereas the anchovy stocks have been most abundant in southern and Baja California (Fig. 3). In the Peruvian case, the anchoveta fishery was largest in northern and central Peru, but the recent sardine fishery has extended to southern Peru and northern Chile (G. Sharp, FAO, Rome, pers. comm.). A similar poleward shift in Peruvian fish production, although of unknown species composition, has been indicated for early historic times (Hutchinson 1950, p. 48):

> It is also noteworthy that the rather unproductive region south of Pisco Bay, as far south as Iquique [i.e. southern Peru], seems from the 16th to the early 19th centuries to have been regarded as a more important source of guano than the central Peruvian coast . . . . The only reasonable, though admittedly speculative, explanation of the decline of importance of the southern islands . . . is that minor changes in the dominant hydrographic pattern have occurred, tending to alter the distribution of the centers of abundant fish.

Evidence of sardine abundance during a period consistent with Hutchinson's speculations could be looked for in Peruvian anaerobic sediments. DeVries and Pearcy (1982: Fig. 9) found isolated sardine scales in central Peruvian coastal sediments at depths indicative of the above period.

Further investigation of Peruvian and Chilean coastal dry lakes by the methods of Goodman (1972), might elucidate the nature of these biogeographic shifts.

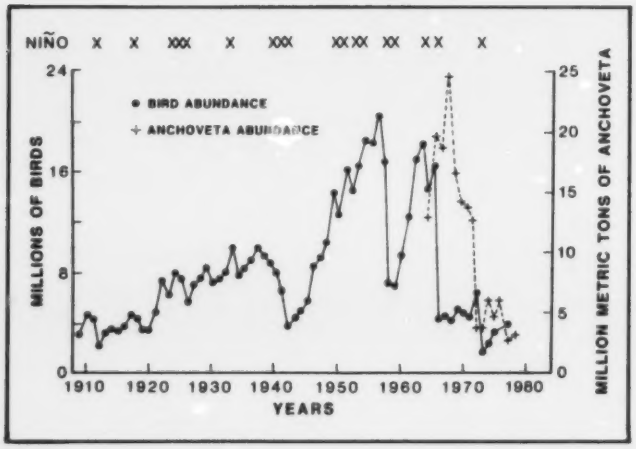
4.4. El Niño

El Niño is an oceanic condition which reaches a unique extreme in Peru. During El Niño the Peru Current episodically weakens, upwelling weakens, and the coast is flooded with warm, nutrient-poor water. A similar but less intense phenomenon occurs in other eastern boundary currents. Mechanisms and physical oceanography of El Niño are discussed by Quinn *et al.* (1978), and biological effects are discussed by Idyll (1973), Valdivia (1978), and Cushing (1981). Biological effects can be severe: reduced primary productivity may lead to fish die-offs, and ultimately to extensive mortality of seabirds, a characteristic sign of El Niño. Ashmole (1971) observes that compared to that of land birds, the life table for seabirds is characterized by low reproductive rate and high survivorship. Duffy (1980) speculates that the high food availability punctuated by severe shortages during El Niño give Peruvian seabirds an unusual life table with high reproductive rate and low survivorship.

El Niño events can be seen in the history of Peruvian guano production and/or guano-bird abundance (Fig. 5). As Idyll (1973), Duffy (1980), and others have observed, El Niño-related population declines have been more severe since the initiation of the anchoveta fishery, and population recoveries have been weak. This decrease in the resilience of the Peruvian guano birds appears to be the result of the fishery having reduced the availability of forage, both through a general reduction in anchoveta abundance, and through direct competition for available surface schools.

Hutchinson (1950:373) and Murphy (1954) have suggested that a nutrient gradient may exist in waters around guano islands, fertilizing the area, and eventually enhancing local fish abundance. This speculation takes on greater potential when El Niño conditions are considered. The Peruvian coast is normally lacking in rainfall, but during El Niño the coast may become subject to tropical downpours which have been termed "disastrous" to the guano industry (Murphy 1954), due to large amounts of guano washed into the sea. This local nutrient enrichment could be substantial under the nutrient-poor conditions of El Niño, and any attraction of fish would undoubtedly improve the foraging prospects of the seabirds inhabiting the islands, and might improve survival conditions for the fish as well. Both Hutchinson (1950) and Murphy (1954) remark that guano birds tend to retain their feces until they return to their island (although no actual evidence was given). This has usually been interpreted as contributing to improved nesting substrate, but it might also contribute to long-term forage stability and increased survivorship through the forage enhancing mechanism hypothesized above. Although this hypothesis is admittedly speculative, it could be experimentally tested by maintaining a specified minimum guano thickness on selected islands, such that the full effect of local enrichment could be observed during El Niño events (of course, fishing activity in the area would have to be restricted). Geochemical analysis, combined with past rainfall patterns could produce an estimate of optimal guano thickness, so that harvest of the excess could continue. It would indeed be ironic if overharvesting by the guano industry contributed to the collapse of the Peruvian anchoveta fishery!

Figure 5
Peruvian guano bird abundance estimated from guano production, anchoveta abundance, and occurrence of El Niño in Peru (modified from Duffy 1980, anchoveta abundance from Tsukayama and Alvarez 1980, 1981)



5. Fishery–seabird dynamics

The topic of fishery–seabird dynamics includes two fairly distinct topics: the influence of seabirds on the fishery, and the influence of the fishery on seabirds. Some aspects of these relationships have been qualitatively touched upon in the preceding discussion. The remainder of this paper will attempt to examine these relationships quantitatively.

5.1. Impact on the fishery

Furness (this volume) has reported that seabirds in several ecosystems may consume 20 to 30% of local annual pelagic fish production. This represents a potentially large increased fishery catch if numbers of birds were to be reduced. Calculations of this sort have been made for the Peruvian anchoveta fishery by Schaefer (1970), who treated the guano birds as a competing fishing fleet. Schaefer estimated that the early-fishery (i.e. 1960–63) bird population of 16 million may have consumed about 2.5 million metric tons of anchoveta per year, or about one-third the amount of the fishery. Jordan (1967) also estimated the early-fishery anchovy consumption by birds to have been between 1.8 and 2.8 million metric tons annually. This consumption rate corresponds to 28% of the initial abundance of anchoveta. This level of fish consumption is likely to have had an effect on forage abundance, and may have been a contributing factor regulating pre-fishery bird abundance. As the anchoveta fishery expanded and the bird populations declined, anchoveta harvest shifted directly from the birds and associated guano industry to the fishery.

Cushing (1981) has performed similar calculations for the quantity of anchoveta in the incoming or "recruiting" age group consumed by the seabirds. Again, the fishery catch effectively replaced anchoveta consumption by the declining seabird population. Cushing assumes the birds to have eaten mainly smaller anchoveta in the recruiting age group. This assumption is consistent with Jordan (1967) who notes that the birds consumed somewhat smaller fish than were taken by the fishery. Cushing (1981) concludes

that the change in seabird consumption of recruits distorted the apparent anchoveta stock-recruitment relationship, giving a false appearance of being dome-shaped.

Consumption of fish by seabirds inhabiting the California Current has not been fully calculated. Wiens and Scott (1975) modelled the seabird–forage relationships off Oregon, and concluded that the birds may consume as much as 22% of the local annual production of pelagic fishes. A large fraction of the total consumption was attributed to the numerous Sooty Shearwaters (*Puffinus griseus*) that pass along the Oregon coast during their migrations. A more ambitious attempt at calculating overall seabird consumption of forage in the California Current was made by Green (1978). Lacking precise estimates of seabird abundance or forage requirements, Green arrived at a tentative total seabird forage consumption of 230 000 – 630 000 t per year, with 140 000 – 380 000 t of that being small pelagic schooling fishes such as anchovy. This "educated guess" corresponds to less than 10% of recent anchovy biomass, leading to the conclusion that seabirds probably are not a major source of anchovy mortality in the California Current. Seabirds also consume large amounts of juvenile rockfish (*Sebastes* spp.) but impact on that resource has not been quantified (Ainley *et al.* 1981).

5.2. Impact on the seabirds

Fishery impacts on seabird populations, presumably through trophic interactions rather than direct mortality, have been inferred for Peru (Schaefer 1970, Anon. 1974, Duffy 1980), and for South Africa (Crawford and Shelton 1978, Burger and Cooper, this volume). Although it has long been accepted that seabird reproductive success is sensitive to food availability (e.g. Ashmole 1971), this relationship has been difficult to demonstrate directly, due to lack of long sets of observations and difficulty in independently measuring food availability. Hunt and Butler (1980) have shown reproductive responses to southern California anchovy abundance in Western Gulls (*Larus occidentalis*) and in Xantus' Murrelets (*Endomychura hypoleuca*). Anderson *et al.* (1982) have shown that Brown Pelican fledging rates in southern California vary with anchovy availability. In Peru, fledging rates of guano birds during the intense fishery, 1966–71, were half the level observed during the early fishery, 1960–63 (Anonymous 1974).

Importantly, reproductive success may not vary smoothly with changes in food availability. Anderson *et al.* (1982) found that Brown Pelican fledging rates appear to decrease sharply below a threshold level of anchovy abundance. Using Ringed Turtle Doves (*Streptopelia risoria*) fed to satiation as controls, Keith (1978) found that if food were limited to 90% of that required for satiation, production fell to 50% of the central level. Production was near zero for birds restricted to 70% of the food required for satiation. If such a threshold response is common in seabirds, effects of lowered forage availability may be very difficult to predict unless the threshold level has been crossed and observed.

Animal populations are usually assumed to have some compensatory mechanism so that reproductive rates tend to increase as a response to lowered abundance. Such mechanisms are poorly documented for seabirds. Ashmole (1971) lists several likely mechanisms, but quantitative data are generally lacking. Again, without knowledge of compensatory capacity we cannot assess the resilience of seabird populations to lowered food availability and possible consequently lowered bird abundance.

5.3. A simulation model

In view of our lack of knowledge regarding the mechanisms regulating seabird reproduction and abundance, it is difficult to predict the effects that particular fisheries may have on particular seabird colonies. However, there is enough information to construct a simple simulation of a hypothetical fishery–seabird interaction. To the extent that the component processes are reasonable models, the "predictions" of the simulation model may provide useful insight into the likely nature of actual fishery–seabird interactions.

The simulation model is intended to mimic fish and seabird dynamics, exemplified by the anchovy and the Brown Pelican in southern California. The model employs several functional sub-models representing components such as age structure, reproduction, and food supply. These sub-models are arbitrary; choices of functions and parameter values are subjective. Some parameter values are constrained by others due to mathematical necessity.

The life table of the model seabird has a constant survivorship schedule, but variable *per capita* reproduction (R). The Leslie matrix, which approximates that of the California Brown Pelican (see Anderson and Gress 1983), is as follows:

0	0	0	R
0.5	—	—	—
—	0.75	—	—
—	—	0.85	0.90

As is shown by the right-hand column, maturity is achieved at age four years. Subadults make no reproductive contribution. All adults experience the same survivorship and reproductive success; there is no maximum age constraint, but the average remaining life span of an adult is 10 years. Birds are censused at the time of fledging, and adult abundance at that time is considered equivalent to the number that attempted breeding.

The per capita reproductive rate is determined by $R = f(F)g(N)$, where $f(F)$ denotes a function of food availability, and $g(N)$ denotes a function of bird population size. In effect, the function $g(N)$ determines the maximum possible per capita reproductive rate averaged over all adults for a given population size, and the function $f(F)$ determines what portion of that potential maximum is realized due to the constraint of food supply. Note that per capita reproduction (here termed "reproductive success") is equivalent to the number of offspring fledged per breeding pair.

Two arbitrary functions, one linear and one non-linear, were used to model the effect of density or population size; both were calibrated to provide a replacement level of reproductive success (1.07) at a population size (N) of 1000 adults, given unlimited food availability, and to provide a maximum reproductive success (mean of all breeding birds, including survival to age one) of approximately 1.7 near zero density (Fig. 6). The parameter values chosen

here are arbitrary; no special significance should be attached to them. The linear model was as follows:

$$g(N) = 1.70 - 0.00063N \text{ if } 0 < N < 2698 \text{ and}$$
$$g(N) = 0 \text{ if } N \geq 2698$$

The latter constraint is necessary to prevent negative reproductive success. The non-linear model was in the form of a "reversed" logistic curve (Fig. 6):

$$g(N) = 1.72/[1 + \text{EXP}\,(0.00394N - 4.44)]$$

This shape of curve was chosen for two reasons. First, Murray (1979), Fowler (1981), and others have argued that many higher organisms, such as large mammals and birds tend to show density-dependent effects mainly at high population levels (close to carrying capacity). Second, it is unlikely that reproductive success would actually approach zero for populations in excess of carrying capacity, rather it should simply fall progressively farther below replacement.

The function used to model the effect of food availability must have a lower bound of zero, an upper bound of unity, and be capable of showing a threshold response at intermediate food levels. Again, a logistic function has these qualities (Fig. 7):

$$f(F) = 1.0/[1 + \text{EXP}\,(-4.39225\,F/W)]$$

where F is a measure of food availability, scaled so that a value of $F = 0$ gives $f(F) = 0.5$. Parameter W controls the steepness of the threshold, so that if $W = 1$, $f(F)$ rises from 0.1 to 0.9 over the interval $F = [-0.5, 0.5]$, a "width" of one unit of F. Values of $W = 0.5$ and $W = 2$ reduce or expand the width of the threshold accordingly, while the centre of the response curve remains at $F = 0$.

Food availability is modelled as a serially correlated, normally distributed random variable with unit variance (Fig. 7). This simulates the approximately normal probability distribution and temporal structure seen in log-transformed anchovy abundance from previous models (Fig. 2). Serial correlation was obtained by use of the recursion algorithm (Yevdjevich 1966),

$$F_t = \rho_s F_{t-1} + r_t (1 - \rho_s^2)^{1/2}$$

where F_t is log food availability in year t, ρ_s is serial correlation coefficient, and r_t is an independent normal N(0,1) random number for each year. This food-availability model does not specify whether a single-species or a multiple-species forage-base is represented. Both cases should behave similarly, except that a multiple-species forage-base may have a relatively smaller variance. It is unnecessary to consider a range of variances in the model food supply because equivalent effects can be obtained by varying the threshold steepness or "width" parameter W in the function $f(F)$.

This model of food availability has a mean value of zero. The effect of changes in mean food supply, perhaps due to fishery or other impact, is modelled by adding an appropriate constant. For example, because F is in logarithmic units, halving of the average food availability can be simulated by adding $\log_e(0.5) = -0.69$.

The model is implemented with an initial equilibrium population structure of 535, 268, 187, and 1000 for ages one, two, three, and adult respectively. As a result, random variability is not seen in the adult abundance until 4 years have elapsed. Due to the high survival rate of adults, the initial abundance of adults may influence results for decades, especially if the initial abundance is far from the eventual equilibrium.

The simulation model was used in two ways. The first way was to follow the time-course of adult bird abundance starting with initial conditions, giving a qualitative impression of patterns and trends. The second way was to determine probability distributions at long-term equilibrium. In the latter case, the simulation was run for 500 years

Figure 6
Alternative linear and non-linear models for maximum average reproductive success (function g(N), see text). Success is equivalent to the number of offspring fledged per breeding pair

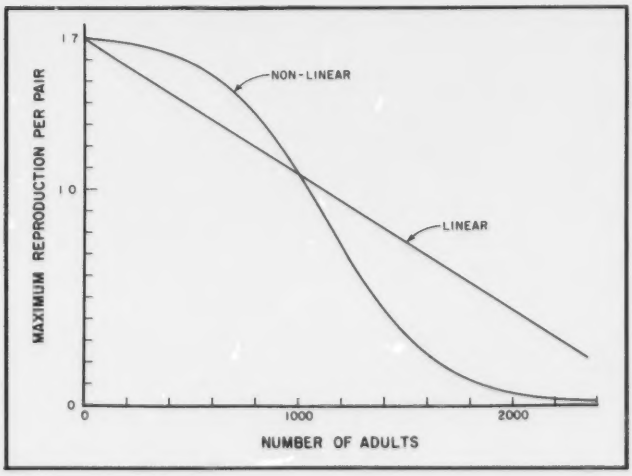
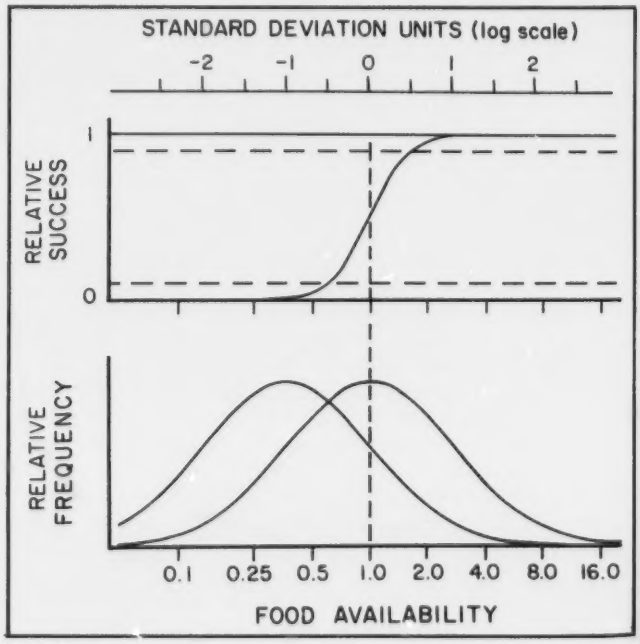


Figure 7
Upper diagram: Food availability threshold ($W = 1$) for relative reproductive success (function f(F), see text). Horizontal dashed lines are 0.1 and 0.9 levels. Lower diagram: Probability distributions of relative food availability ($\sigma = 1$). Right probability curve represents possible virgin distribution ($\bar{F} = 1$), left probability curve represents possible distribution under exploitation ($\bar{F} = 0.37$). Note that food availability is arbitrary

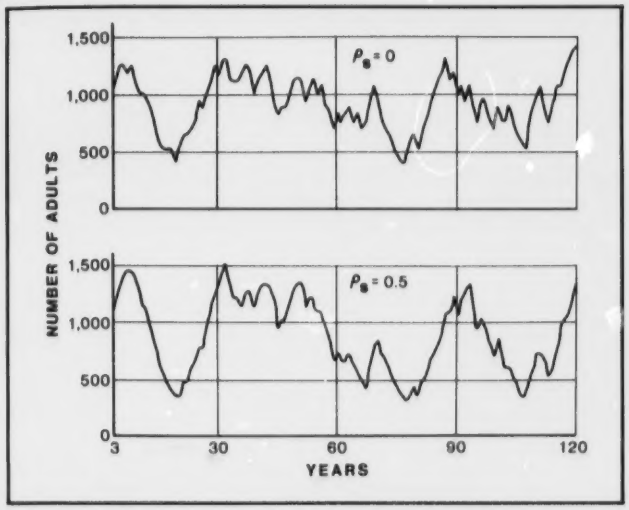


to establish equilibrium before monitoring the results. All simulations used the same series of random numbers (r_t).

5.4. Simulation results

This model was designed to investigate the fundamental question of how seabird abundance may vary as a function of characteristics of seabird food supply. Although the mean level of food availability is probably the most important factor, the variance and serial correlation of the food supply also impact the bird population.

Figure 8
Simulated time-series of seabird abundance for two levels of serial correlation (ρ_s) in food availability ($\bar{F} = 1$, $W = 1$, $\sigma = 1$, non-linear reproduction model)



As described earlier, serial correlation is a measure of similarity of food availability in successive years. The effect of serial correlation of the food supply can be seen in comparative population trajectories (Fig. 8). Increased serial correlation preserves the overall pattern, but the excursions to high and low levels of abundance become more severe. The equilibrium probability distributions (Fig. 9) show that the bird population varies only moderately about the mean for a serially uncorrelated food supply, but in the presence of serial correlation there are occasional excursions to near-extinction. The long-term mean abundance is only slightly affected by serial correlation, as the magnitude and duration of excursions to high and low abundance nearly balance.

The effect of variance in food supply has surprisingly similar effects to those of serial correlation (Fig. 10). High variance (equivalent to a very sharp threshold) generates high population variability, whereas low variance enables the population to remain near mean abundance. Again, the effect of increased population variability is only a slight lowering of long-term mean abundance. The above simulations were for a mean food abundance centred at the mid-threshold level. Clearly, the effective variance in bird response will decrease as the mean food abundance moves above or below this threshold level. In effect, the birds will more consistently be successful or unsuccessful. If a sharp threshold response to food availability is to be expected for seabirds, these results indicate that its delineation is very important to predicting fishery impacts.

Figure 9
Long-term probability distributions of simulated seabird abundance for three levels of serial correlation, (ρ_s) in food availability ($\bar{F} = 1$, $W = 1$, $\sigma = 1$, non-linear reproduction model). The arrow indicates mean abundance

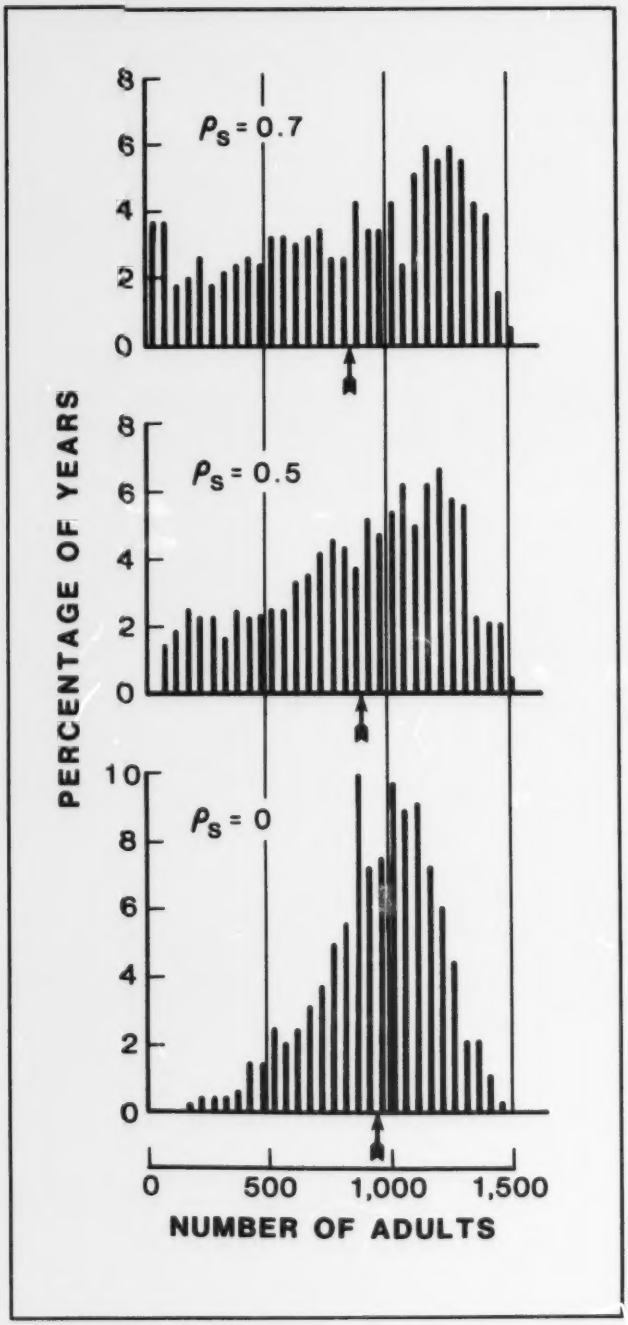
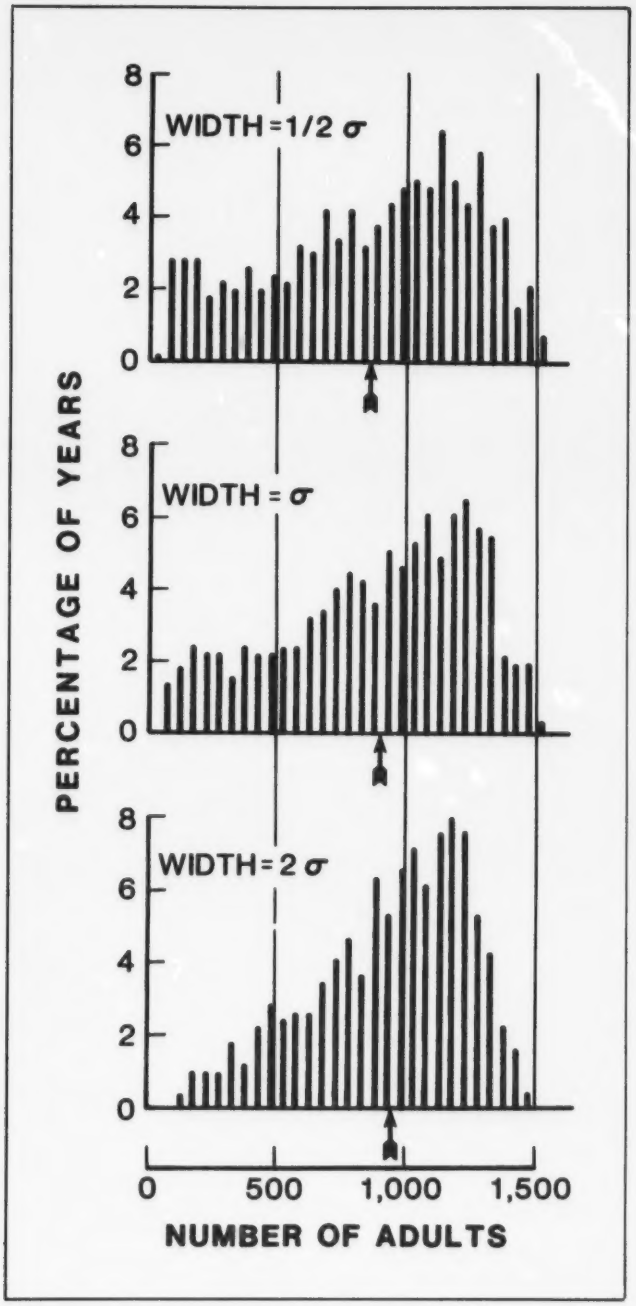


Figure 10
Long-term probability distributions of simulated seabird abundance for three threshold sensitivities (widths) to food availability ($\bar{F} = 1, \sigma = 1$, $\rho_2 = 0.5$, non-linear reproduction model). The arrow indicates mean abundance



Variance and serial correlation of the food supply appear to have little effect on the long-term mean bird abundance, however the mean food supply itself has the anticipated relationship to mean bird abundance. Mean bird abundance declines as mean food availability declines (Fig. 11), but there is an unexpectedly sudden drop in mean bird abundance near the critical food level causing extinction. This sharp drop is more severe for the non-linear model than the linear model, apparently due to the non-linear response having exhausted its compensatory capacity near the virgin level (see Fowler 1981). On an arithmetic scale, the drop is more precipitous than on the logarithmic food-availability scale of Figure 11.

The virgin level of food abundance is defined only relatively in this model. Several possibilities can be examined. In terms of fishery impact, it is useful to assume that a "well-managed" fishery will reduce fish availability to about one-half its unexploited level. In the face of such a fishery impact, the bird population will survive if the unexploited food level is above about 1.4 relative units (Fig. 11), assuming no serial correlation of food supply. This result suggests that those seabird populations showing sporadic reproductive success under pre-fishery conditions may be severely impacted by a fishery on their food supplies. Unfortunately, many seabirds outside of Peru seem to fall into this category.

Although it is clear from Figure 11 that the model seabird can exist on a mean relative food availability of 1.0, but will become extinct on a mean food supply of 0.5, this fact would not immediately be clear from an abundance monitoring program. I simulated an example based on 120 years of seabird abundances for these two mean food levels and an initially pristine bird population: the patterns obtained were disturbingly similar (Fig. 12). Because of high serial correlation, the true long-term trend tends to be masked by prolonged variability at intermediate time scales of decades. In both cases there would be apparent cause for alarm during the first 20 years of the fishery, but the birds would stage an apparent recovery due to a more favourable environment over the subsequent 30 years. From abundance alone, it would not be apparent for over 60 years whether the population is viable. Prediction of fishery impact will require detailed studies of seabird population dynamics as well as improved fishery models. Unfortunately the long trends in seabird and fish populations associated with high serial correlations indicate that short-term studies are likely to miss upper or lower ranges of abundances which may be important to understanding long-term dynamics.

Many modifications of this simple model are possible, and until most of the reasonable cases have been examined, it would be unwise to attempt broad generalizations. It is not within the scope of this paper to attempt such a complete investigation. Other life tables have not been considered here because it would be difficult to establish a simple standard of comparison. Higher adult survival rates would require lower average reproductive success to maintain comparable population levels. However, the nature of such a change is easy to anticipate. In this model, bird abundance behaves as a moving average of fish availability, with exponentially declining weights. Higher survival would increase the span of time over which averaging occurs, and would tend to decrease the variability of seabird abundance.

Simulation modelling of a Peruvian seabird population may require three modifications. The probability distribution of the food supply should reflect sudden declines typical of El Niño; this pattern is not well modelled by the simple serial correlation algorithm used here. Also, predation pressure from the seabirds themselves might modify the availability of food. Finally, the life table would have to contain variable survival rates, perhaps dependent on food availability, to reflect the mortality that occurs during El Niño events. These investigations are beyond the scope of the present paper.

Figure 11
Long-term mean simulated seabird abundance in relation to mean food availability ($\bar{F}$) for two alternative reproduction models ($W = 1, \sigma = 1, \rho_r = 0.5$, non-linear reproduction model)

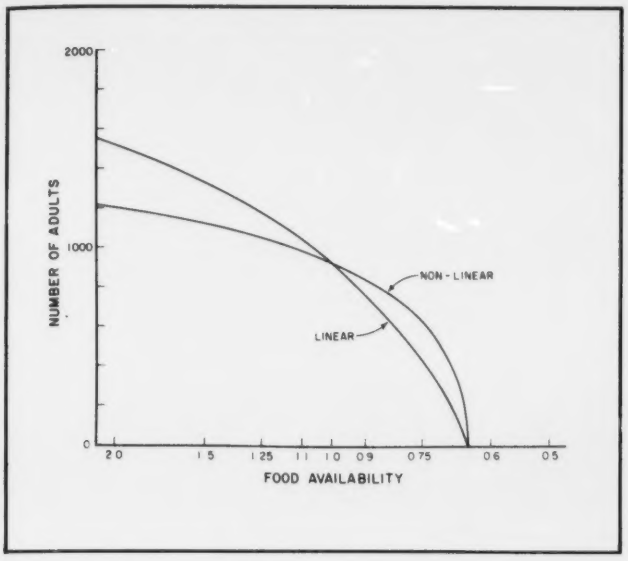
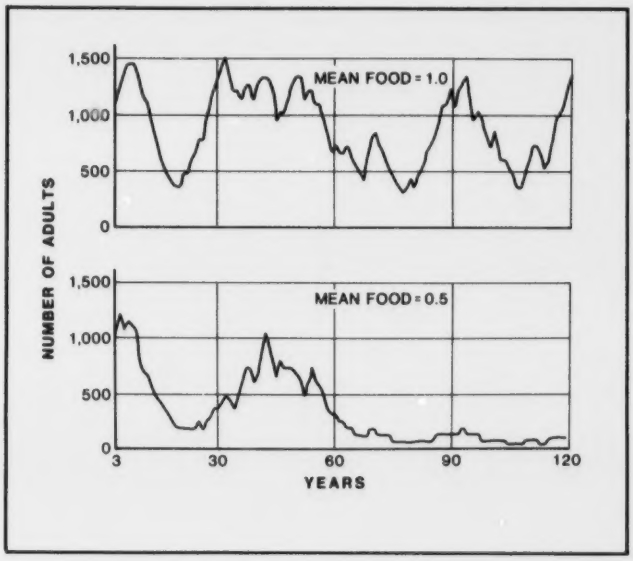


Figure 12
Simulated time-series of seabird abundance for two levels of mean food availability ($\bar{F}$ = mean food, $W = 1, \sigma = 1, \rho_r = 0.5$, non-linear reproduction model)



6. Conclusion

The relationship between seabird abundance and fishery activity cannot be considered outside the context of natural patterns of forage availability. Those patterns are superficially similar in California and Peru, but Peru is different in two important, interrelated respects. In the absence of an intense fishery, forage availability is much higher in Peru, but the episodic occurrence of El Niño causes more severe shortages than are observed in California. Because of these differences, the potential impacts of fisheries on seabird abundance are not necessarily comparable. The California and Peruvian fisheries are likely to impact the life table and regulatory mechanisms of the seabirds in different ways.

As more details of seabird life history and population dynamics become known, it may be possible to construct more useful models of seabird–fishery relationships. Also, improved models of the erratic temporal and geographic behaviour of the fish resources should improve the utility of seabird–fishery interaction models. The present attempt relies on an overly simple "black box" representation of these important components. The results of this exercise are suggestive, but should not be taken without reservation; yet the indication that seabirds may be slow in overall population response, but very sensitive to chronic forage depletion, should be considered in the determination of optimum fishery yields. The long life span of seabirds may allow sufficient time to gain understanding of trophic interactions so that appropriate action may be taken before species are actually endangered by prolonged reproductive difficulties. The developed countries are showing increased concern for maintaining the diversity of species in the natural environment. Let us hope that this trend reflects a movement toward human cultural maturity rather than a passing luxury allowed by inexpensive fuel and relatively abundant food.

7. Acknowledgements

I wish to thank the many who have contributed to this paper, but especially Dan Anderson, who introduced me to seabird biology, and who encouraged this work. I also thank Andy Bakun, some of whose original ideas on the relationship of El Niño, guano, and coastal productivity are discussed here. Finally, this study would not have been produced without the support and facilities of the Southwest Fisheries Center, La Jolla, California.

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The effects of fisheries on seabirds in South Africa and Namibia

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1. Abstract

Seabirds have been affected by two major fisheries in South Africa and Namibia (South-West Africa). Demersal trawlers operating at the continental shelf edge provide large amounts of food to seabirds, mainly non-breeding migrant procellariiforms. The effects of this fishery on seabird populations are not yet known. The purse-seine fishery removes the same pelagic fish species as Jackass Penguins (*Spheniscus demersus*), Cape Gannets (*Sula capensis*), and Cape Cormorants (*Phalacrocorax capensis*), and operates within the same areas as these birds. Intensive purse-seining in the 1960s and 1970s caused significant decreases in several fish stocks, notably those of the pilchard (*Sardinops ocellata*) and horse mackerel (*Trachurus trachurus*), and a decrease in the average size of fish available. These changes had major effects on certain seabirds. Census data, supplemented by records of guano harvests, indicated substantial changes in the populations of the Jackass Penguin, Cape Gannet, and Cape Cormorant, which may be attributable to changes in prey availability. The diets of these three species also changed markedly between the mid 1950s and 1978–80. Some seabird species were more resilient to the changes than others. Jackass Penguins probably have been most severely affected by the purse-seine fishery. Many seabird species do not eat commercially important organisms and have not been affected by the fisheries. We discuss possible limiting factors of seabird populations, and emphasize a need for investigation into limiting factors in order to plan meaningful conservation measures for seabirds.

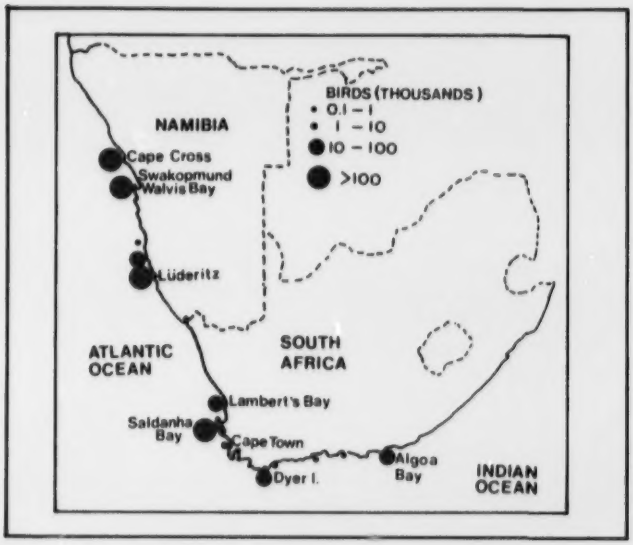
2. Résumé

Deux types de pêche importants ont influé sur les populations d'oiseaux de mer en Afrique du Sud et en Namibie (sud-ouest de l'Afrique). Les chaluts de fond qui opèrent au bord du plateau continental fournissent de grandes quantités de nourriture aux oiseaux de mer, principalement aux procellariiformes migrateurs qui ne nichent pas dans la région. Les effets de cette pêche sur les populations d'oiseaux de mer restent encore inconnus. La pêche à la senne coulissante prélève les mêmes espèces de poissons pélagiques que le Manchot (*Speniscus demersus*), le Fou du Cap (*Sula capensis*) et le Cormoran du Cap (*Phalacrocorax capensis*) et se déroule dans les mêmes régions fréquentées par ces oiseaux. La pêche intensive à la senne coulissante dans les années 1960 et 1970 a réduit considérablement les stocks de poissons, notamment ceux du pilchard (*Sardinops ocellata*) et du chinchard (*Trachurus trachurus*), et a entraîné une diminution de la taille moyenne des poissons disponibles. Ces changements ont eu des effets dramatiques sur certains oiseaux de mer. Les données du recensement, complétées par des relevés de récolte du guano, révèlent l'existence de profondes modifications dans les populations du Manchot, du Fou du Cap et du Cormoran du Cap, qui doivent être attribuables à des variations de la disponibilité des proies. Les régimes alimentaires de ces trois espèces ont également changé de façon spectaculaire entre la moitié des années 1950 et 1978–1980. Certaines espèces ont mieux résisté aux changements que d'autres. C'est le Manchot qui a probablement souffert le plus de la pêche à la senne coulissante. De nombreuses espèces d'oiseaux de mer ne consomment pas d'organismes d'importance commerciale de sorte qu'elles n'ont pas été touchées par la pêche. Nous examinons certains facteurs limitatifs possibles de la population d'oiseaux de mer et soulignons le besoin d'études sur ces facteurs pour pouvoir planifier des mesures de conservation mieux articulées en faveur des oiseaux de mer.

3. Introduction

Seabirds and people compete for fish off the coast of southern Africa. The upwelling of the Benguela Current and inshore upwelling and mixing produce areas of high productivity (Cushing 1971, Crawford 1980) which support very large numbers of seabirds (Fig. 1) and a large commercial fishery. The first intensive research into seabirds was undertaken in this region in the 1950s, mainly to estimate the effects of seabird predation on the commercial fish stocks (Davies 1955, 1956; Rand 1959, 1960*a*, 1960*b*, 1963*a*, 1963*b*; Matthews 1961). These studies suggested that certain seabirds did eat commercially important fish species. Some form of control of seabird populations was recommended (Davies 1958) but never implemented. During the past decade, however, biologists have been increasingly concerned about the consequences of intensive fishing on the populations of seabirds (Frost *et al.* 1976; Crawford and Shelton 1978, 1981; Cooper *et al.* 1982; Cooper, 1984; Furness and Cooper 1982). In addition, fisheries biologists have become interested in the analysis of seabird population trends, breeding success, and dietary changes as possible indicators of available fish stocks (Crawford and Shelton 1978, 1981; Newman and Crawford 1979). As a result, seabird research has become increasingly popular at South African universities and research institutes. Understanding of the seabirds in the region has increased considerably, although the feeding behaviour of many species is still poorly known. This paper reviews the recent studies of the population sizes and diets of selected species of seabirds in

Figure 1
Distribution of the major seabird colonies in South Africa and Namibia. (South-West Africa). The greatest number of seabirds breed within the Benguela Current system of the Atlantic Ocean. Census data from references quoted in the text



South Africa and Namibia (South-West Africa) and the effects of commercial fishing on these seabirds.

People and seabirds have a long history of interaction in southern Africa. The hunter-gatherers who frequented the Cape coast for many thousands of years relied quite extensively on beached seabird carcasses for food in certain seasons (Avery 1977). Settlers from Europe began exploiting seabirds over 300 years ago. Eggs and guano were the principal products harvested. Disturbance and over-exploitation led to the extinction of some colonies of Jackass Penguins (*Spheniscus demersus*) (Westphal and Rowan 1971, Shaughnessy and Shaugnessy 1978) and the drastic reduction in size of others (Frost *et al.* 1976). Egg-collecting has now been halted. Harvesting of adults and chicks has not been common in the past century, although sporadic killing of adult seabirds at sea for human food still occurs (Cooper 1977).

The collection of guano has also affected the seabirds. The huge accumulated deposits of guano capping the offshore islands were removed by 1845 (Jarvis 1970) thereby changing the characteristics of the seabird colonies. Jackass Penguins, which dug burrows into the guano, lost optimal nesting sites (Berry *et al.* 1974, Frost *et al.* 1976). Harvesting of the annual deposits continues to the present, with mixed consequences for seabirds. The harvest destroys many of the eggs, chicks, and nests of late breeders, but the protected status of the guano islands might have reduced other human disturbances. At several sites in Namibia, large wooden platforms have been built to collect guano deposited by breeding and roosting seabirds. The platforms, with a total area of 10 ha, have been very effective and over 100 000 Cape Cormorants (*Phalacrocorax capensis*) now breed regularly in areas with no suitable islands (Berry 1976*a*, Crawford and Shelton 1981). Guano-harvesting has become less profitable recently and has ceased on a number of islands. Penguin guano is no longer collected.

African seabirds are affected by other human actions. Pollution of the sea by petroleum has led to high seabird mortality on several occasions, and is a potential threat to the population of Jackass Penguins (Westphal and Rowan 1971, Frost *et al.* 1976, Morant *et al.* 1981). Fish-oil pollution (Anon. 1974, Berry 1976*b*) and harbour development (Jarvis 1970, Anon. 1973, Brooke *et al.* 1982, Crawford *et al.* 1982*a*) have also affected seabirds.

Intensive commercial fishing now appears to be the greatest single threat to the populations of some seabird species in southern Africa. Evidence reviewed below shows that the overall abundance of certain populations of prey has been reduced by fishing in several areas, while the proportions of prey species and the size of fish available have been altered in most areas. This has coincided with noticeable changes in the population sizes and diets of some species of seabirds.

4. Seabird species in southern Africa

Approximately 65 species of seabirds have been recorded within territorial waters off South Africa and Namibia (Brooke 1981). These include 14 species that breed on these shores and about 20 species that commonly occur as non-breeding visitors.

Estimates of the populations of the locally breeding species vary (Crawford and Shelton 1978, 1981; Cooper 1984) but at least 700 000 individuals breed annually within the region. Over 95% of these birds are Jackass Penguins, Cape Cormorants, and Cape Gannets (*Sula capensis*) (Crawford and Shelton 1978). These three species all prey predominantly on fish, particularly the pelagic shoaling species which are of commercial importance (Crawford and Shelton 1981, Batchelor 1982, Cooper 1984). Since they are the most common species and eat commercially important fish, these birds have been studied most intensively and they are the main focus of this review.

The fishing industry appears to have little impact on the feeding of Bank Cormorants (*Phalacrocorax neglectus*), Whitebreasted Cormorants (*P. carbo lucidus*), Crowned Cormorants (*P. coronatus*), and the four species of resident terns. These birds tend to prey on marine organisms that are of little or no commercial interest to people (Rand 1960*b*, Randall and Randall 1978, Cooper 1981, Brooke *et al.* 1982, Crawford *et al.* 1982*b*). More intensive research might reveal that the diets of some of these species might be affected by the fishery now or in the future. The Great White Pelican (*Pelicanus onocrotalus*) breeds in small numbers on islands and platforms on the coast but it does not always feed at sea. The gulls that breed on the coast may have benefited from the fishery (Crawford *et al.* 1982*a*). Kelp Gulls (*Larus dominicanus*) and Hartlaub's Gulls (*L. hartlaubi*) are common scavengers at fish-processing factories and Kelp Gulls at fishing vessels.

The sea off southern Africa also supports large numbers of non-breeding migrants from the northern hemisphere and the southern ocean. The greatest numbers are terns from the northern hemisphere and albatrosses, shearwaters, and petrels (Order Procellariiformes) from the south. These birds are beginning to get serious attention from biologists in southern Africa, with attempts being made to obtain quantitative data on their densities, distributions, and feeding behaviour (Summerhayes *et al.* 1974, Cooper and Dowle 1976, Abrams and Griffiths 1981, Griffiths 1981, Abrams 1983).

5. Changes in the fish populations

Two major fishing methods have affected seabirds: purse-seining in inshore waters and demersal trawling at the continental shelf edge.

Purse-seining is used to catch pelagic shoaling fish, including pilchard (*Sardinops ocellata*), anchovy (*Engraulis capenis*), horse mackerel (*Trachurus trachurus*), mackerel (*Scomber japonicus*), round-herring (*Etrumeus teres*), and other species. Intensive purse-seining began in the mid 1940s and rapidly developed into one of the larger industries of this kind in the world. In South Africa and Namibia this intensive fishing produced changes in the population size and age-structure of certain fish stocks. Most of these fish species are migratory, and various age-classes of a species often have different distributions (Crawford 1980). Certain species also have two or more independent populations. For example, the population of pilchards off South Africa is apparently independent of the Namibian population (Crawford 1981*a*).

Off South Africa the purse-seiners concentrated initially on pilchard and horse mackerel but later developed a multi-species fishery. To a certain extent the annual fluctuations in the catches of the different species were out of phase, so that the total annual catch remained fairly stable, although by the 1960s and 1970s there was good evidence of overexploitation of certain populations (Newman and Crawford 1979). Pilchard landings reached a peak in the years 1960–63 (Fig. 2) following exceptionally strong recruitment between 1956 and 1959 (Newman and Crawford 1980, Crawford 1981*a*), but decreased dramatically from 1964 to 1967. Catches of horse mackerel decreased 100-fold in 20 years and have not recovered (Fig. 2). Much of the increased fishing effort was diverted to anchovies (Fig. 2), with a reduction in the net mesh diameters from 32 to 12.7 mm in 1963–65 (Crawford 1981*a*). Currently, anchovies are the most commonly caught shoaling fish off South Africa. Over half the catch comprises fish of one year old or less and Crawford 1981*b* suggested that older anchovies were infrequently accessible to seabirds due to their migratory movements and the effects of the fisheries. Small pilchards, 2–4 years old, are still seasonally abundant on the south and east coasts of South Africa, but the older pilchards which were once abundant on the west coast have been "virtually eliminated" (Crawford 1981*a*, 1981*b*).

Similar trends occurred off Namibia (Fig. 3). The intensive exploitation of pilchards in the late 1960s led to a collapse of the stocks in 1971. The stocks recovered partially in 1973–74, but decreased again in 1976 (Cram 1978). The pilchard catch exceeded 1.3 million metric tons in 1968, which was well in excess of the 0.8 million metric tons estimated to be the sustainable yield (Newman 1970). Intense exploitation of anchovy, which partially replaced pilchard in catches, was followed by a decrease in catches in 1977, when several processing factories were forced to close. Populations of the pelagic goby (*Sufflogobius bibarbatus*) may have increased off Namibia north of Lüderitz in the 1970s (Cruickshank *et al.* 1980). This small shoaling species is of little commercial importance but is now important in the diets of some seabirds (see below).

Coinciding with the changes in fish populations were changes in the size and age structure of some species (Fig. 4) and reductions in egg production (Cram and Visser 1973, Cram 1978, Newman and Crawford 1979, Crawford 1980). These changes appear to be related to overfishing. Currently efforts are being made to diversify the industry, to shift the emphasis of production to more fish for direct human consumption and less fish meal, and to reduce the overall fishing effort (Cram 1978, Newman and Crawford 1979).

Most of the seabirds that breed in southern Africa feed fairly close inshore. For example 85, 95, and 70% of the Jackass Penguins, Cape Cormorants, and Cape Gannets, respectively, feed within 50 km of the coast (Cooper 1984). Since the purse-seine industry operates within the same area, and removes the same suite of fish species as do these seabirds, this fishery is potentially a major competitor of these seabirds (Frost *et al.* 1976; Crawford and Shelton 1978, 1981). The pelagic shoaling fish are also eaten by large populations of Cape fur seals (*Arctocephalus pusillus*) and several species of predatory fish (see references in Crawford 1980).

Figure 2
Annual catches of pilchard, anchovy, and horse mackerel off South Africa, 1950–78, plotted on a logarithmic scale. From Frost *et al.* (1976) with additional data from Newman and Crawford (1979)

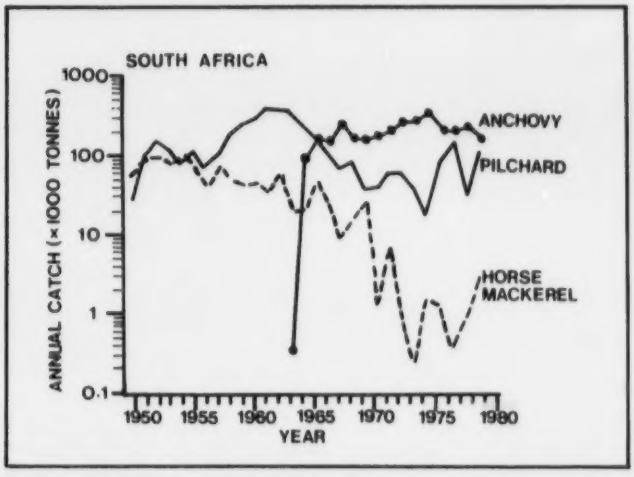


Figure 3
Annual catches of pilchard and anchovy off Namibia, 1950–77, plotted on a logarithmic scale. From Frost *et al.* (1976) with additional data from Cram (1978)

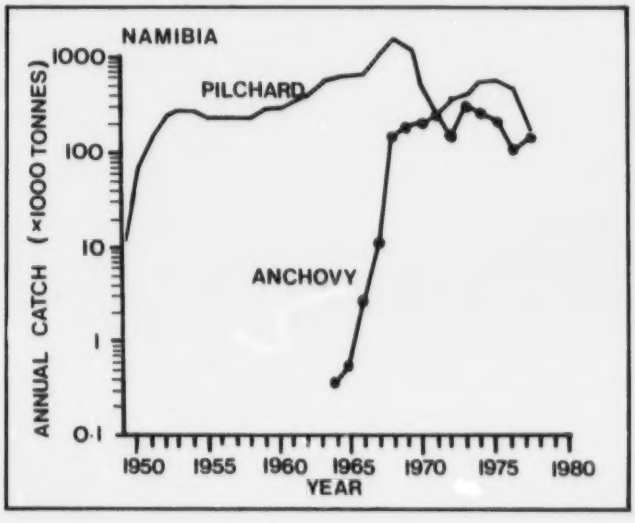
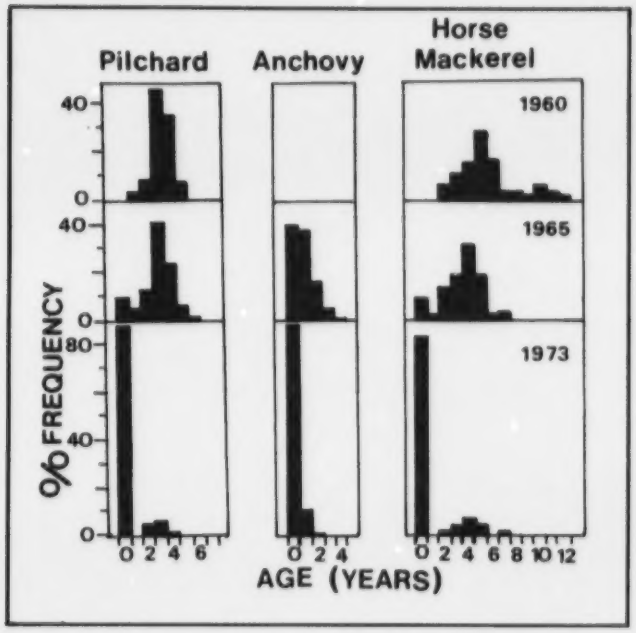


Figure 4
Age composition of pilchard, anchovy, and horse mackerel off South Africa in 1960, 1965, and 1973. From Newman and Crawford (1979)



A second major fishery in southern Africa involves mid- and deep-water stern trawling, usually at the edge of the continental shelf, 90–150 km offshore. Hake (*Merluccius* spp.) are the most common catch. The demersal fish taken by trawlers are not normally freely available to seabirds, but the recent development of this industry has attracted very large numbers of seabirds which eat the netted fish and discarded offal (Sinclair 1978, Abrams 1983, Cooper 1984). The only locally breeding seabirds that regularly visit trawlers are Cape Gannets and Kelp Gulls, but they are greatly outnumbered by albatrosses, shearwaters, and petrels. Jackass Penguins, Cape Cormorants, and other local breeders appear to be precluded from this new food resource by their restricted feeding ranges and inappropriate feeding methods.

Quantitative estimates of the food taken by seabirds from demersal trawlers, and the proportions of this food eaten by each seabird species are not yet available. These trawlers provide a great quantity of food to certain migrant seabirds (Sinclair 1978, Abrams 1983), but it is not known whether this has affected their survival or population sizes.

6. Changes in breeding seabird populations

6.1. Changes detected from colony surveys

Censuses of the major seabird colonies in southern Africa have been sporadic until recently (Crawford and Shelton 1981). Fairly complete censuses were made in 1956 (Rand 1960*b*, 1963*a*, 1963*b*) prior to the intensive exploitation of pelagic shoaling fish. Incomplete censuses were made in 1967–69 and complete censuses in 1978–81 (Crawford and Shelton 1978, 1981). Comparisons of these data show some of the effects of changing fish stocks. Although the population trends are clear, the actual numbers need to be interpreted with caution. Many counts apply to only one

Table 1
Population estimates for Cape Gannets, Jackass Penguins, and Cape Cormorants, 1956–78, in South Africa and Namibia. From Crawford and Shelton (1981)

	Year		
Locality	**1956**	**1967 or 73***	**1978**
Cape Gannet (number of individuals)			
All islands off South Africa	50 913	44 954	97 043
All islands off Namibia	169 656	131 818	88 708
Total population	220 569	176 772	185 751
Jackass Penguin (summer breeding population)			
All islands off South Africa	148 154	Incomplete data	80 166
All islands off Namibia	88 367	48 039	24 184
Total population	236 521	Incomplete data	104 344
Cape Cormorant (number of individuals)			
All islands off South Africa	90 403	No data	177 528
All guano platforms in Namibia	19 984	521 000	112 181
All islands off Namibia	6 161	No data	82 277
Total population	116 548	Incomplete data	371 978

*Data is for 1967 for Cape Gannet and Jackass Penguin and 1973 for Cape Cormorant.

time of year but some of the seabirds have extended or variable breeding seasons. Aerial photography was extensively used and this method does not always give reliable estimates of total breeding populations of all species (Frost *et al.* 1976, Crawford and Shelton 1981).

There were fewer Cape Gannets breeding in 1978 than in 1956, but slightly more than in 1967 (Table 1). Breeding populations at all three gannetries in Namibia decreased, coinciding with a decrease in the biomass of pilchards in that region (Crawford and Shelton 1981). The population counted in Namibia in 1978 was only 52% of that of 1956 (Table 1). Populations at the two gannetries on the west coast of South Africa decreased from 1956 to 1967 but subsequently increased and in 1978 exceeded the 1956 size (Crawford and Shelton 1981). The initial declines followed decreases in the pilchard biomass, whereas recent increases might have been due to increased availability of anchovy to the gannets (Crawford and Shelton 1981). Gannet numbers at the colony on Bird Island, Algoa Bay on the east coast doubled between 1956 (40 156 breeding adults) and 1977–79 (average over three seasons = 85 838 breeding adults) (Randall and Ross 1979, Batchelor 1982).

Censuses of the summer breeding population of Jackass Penguins indicate a large decrease in the total population (Table 1). The changes were not uniform throughout the bird's range. There were severe decreases at all five colonies south of Lüderitz, Namibia (Fig. 1) which were attributed to the collapse of the local pilchard stocks (Crawford and Shelton 1981) and, at one island, to interference from Cape fur seals (Shaughnessy 1980). By contrast, numbers of Jackass Penguins increased at Mercury and Ichaboe islands, north of Lüderitz (Crawford and Shelton 1981), where the birds appear to be exploiting locally abundant pelagic gobies (see below). In South Africa, the large decrease (Table 1) was entirely due to a 50% or greater decrease in the sizes of colonies on the west coast, attributed to low pilchard biomass and apparent failures of the penguins to respond to increased anchovy biomass (Crawford and Shelton 1981). At Dyer Island on the south coast (Fig. 1) the population increased five-fold from 1956 to 1978, and Crawford and Shelton (1981) speculated that this might be due to movements of penguins away from the

west coast to a region where pilchard were still available. Penguin numbers at islands in Algoa Bay (Fig. 1) also increased (Crawford and Shelton 1981), perhaps indicating that food availability was not a serious problem there.

The serious decrease in the population of Jackass Penguins is also evident in the decline in numbers of eggs harvested from islands off South Africa. At Dassen Island, the largest colony off South Africa, over 450 000 eggs were harvested annually between 1900 and 1930, indicating a minimal breeding population of 300 000 adults (Frost *et al.* 1976). In 1978 the population was only 22 440 adults (Crawford and Shelton 1981). Frost *et al.* (1976) concluded that "the decline in the Jackass Penguin population was initiated by prolonged over-exploitation of eggs, together with excessive disruption of breeding birds." Since egg-collecting and guano-harvesting at penguin colonies has now officially ceased, competition with purse seiners is possibly the greatest human threat to the Jackass Penguin (see Section 8: Discussion).

Accurate estimates of the total breeding populations of Cape Cormorants are difficult to obtain (Crawford and Shelton 1981), but the available data indicate an overall increase in the total population since 1956 (Table 1). The increase of Cape Cormorants at guano platforms between 1956 and 1973 (Table 1) was attributed to the construction of a large platform at Swakopmund in the early 1960s (Crawford and Shelton 1981). The subsequent decrease in numbers between 1973 and 1978 was related to the decline in pilchard biomass over this period (Crawford and Shelton 1981). Cape Cormorant populations off South Africa increased after 1956 (Table 1). The numbers at colonies on the west coast increased by 50% or more, while the population at Dryer Island, the only major colony east of Cape Point, increased from 3186 in 1956 to 46 393 birds in 1978 (Crawford and Shelton 1981).

The population of Bank Cormorants appears to have doubled between 1956 and 1978 to a total of 18 000 birds (Cooper 1981, 1984). The increase occurred in Namibia where the Bank Cormorants appear to have benefited from the decrease in Cape Gannet numbers at nesting colonies and the availability of a large population of the pelagic goby (Cooper 1984).

The small population of White Pelicans breeding in coastal Namibia has apparently declined during the late 1960s and 1970s and Crawford *et al.* (1981) have related this to declining local populations of the Cape Cormorants whose eggs and chicks are preyed on by the pelicans.

The populations of Crowned and Whitebreasted cormorants and Kelp Gulls have shown local fluctuations in size historically but no clear overall trends are discernible (Crawford *et al.* 1981, Brooke *et al.* 1982, Crawford *et al.* 1982*a*). The Roseate Tern (*Sterna dougallii*) has decreased in numbers, but this is not attributed to changes in prey availability (Randall and Randall 1980). Little or nothing is known about overall changes in the population sizes of other breeding species: Hartlaub's Gulls, Greyheaded Gulls (*Larus cirrocephalus*), Swift Terns (*Sterna bergii*), Damara Terns (*S. balaenarum*), and Caspian Terns (*S. caspia*). Reasonably accurate estimates of present population sizes do exist for these last five species (J. Cooper, unpubl. data).

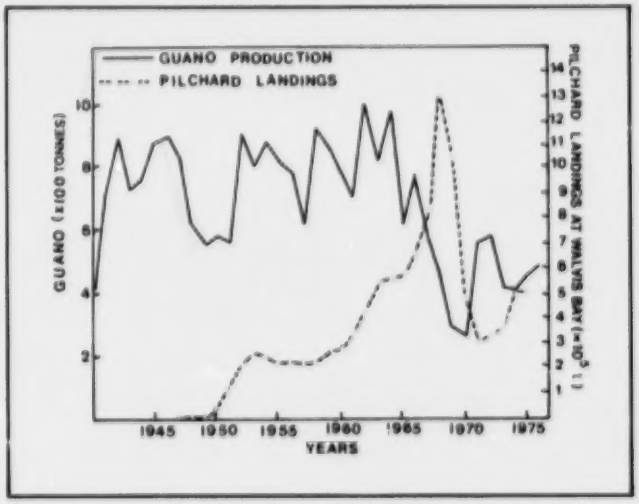
6.2. Changes estimated from guano harvests

In the absence of a long series of censuses of seabird populations, Crawford and Shelton (1978) and Siegfried and Crawford (1978) used the records of the annual guano harvests to monitor population changes of seabirds. Guano records are available from many islands since before 1900. Virtually all of the guano was produced by Cape Cormorants, Cape Gannets, and Jackass Penguins. These records illustrate some of the effects of intensive fishing on seabird populations.

The guano records from the colony of Cape Cormorants at the Bird Rock platform showed the effects of intensive fishing for pilchard on the Namibian coast, near Walvis Bay (Fig. 5). Guano harvests fluctuated widely prior to 1965, then decreased significantly. The decrease coincided with an exponential increase in the landings of pilchards by purse seiners and a corresponding decrease in the catch per unit effort (Crawford and Shelton 1978). Guano harvests correlated significantly with available fish stocks at some other locations too (Fig. 6). Cyclic fluctuations of guano harvests also indicate the possibility of periodic oscillations in the factors affecting seabirds at some colonies (Crawford and Shelton 1978, Siegfried and Crawford 1978).

Crawford and Shelton (1978) found that guano harvests correlated well with known population changes of seabirds at several localities, although this is not always the case. For example, Randall and Ross (1979) showed that the population of Cape Gannets at Bird Island, Algoa Bay, doubled between 1956 and 1978, but the guano harvests actually decreased during this period. Guano harvests were affected by many variables including labour problems and periodic heavy rainfall which washed away guano (Crawford and Shelton 1978, Randall and Ross 1979). Also, non-breeding birds which roosted, and thus defecated, on islands, often greatly outnumbered the breeding birds (Frost *et al.* 1976, Furness and Cooper 1982) and thus guano harvests did not only reflect the breeding populations. The proximity of profitable fish shoals to the breeding colonies would affect the amount of time the birds spent on the islands and thus the amount of guano deposited. Crawford and Shelton (1978) also suggested that variable guano

Figure 5
Guano production from Bird Rock platform near Walvis Bay, Namibia and total catch of pilchard off Walvis Bay, 1940–75. The annual totals of guano have been smoothed by calculating moving averages of 3-year intervals. From Crawford and Shelton (1978)



harvests might reflect changes in breeding success of the birds, and that the effects of food shortages on adult populations might be deferred. Despite some reservations, guano harvests are useful indicators of the effects of intensive fishing on seabird populations.

Guano harvests from all the South African islands combined, showed wide fluctuations prior to 1950, reduced fluctuations from 1950–62, and a significant decrease since 1962 (Fig. 7). These changes coincided with the onset of intensive purse-seining in the 1950s and the severe reductions in certain fish stocks, notably pilchards, in the 1960s and 1970s (Crawford and Shelton 1978). Guano harvests from Namibia likewise showed reduced fluctuations since the 1950s, but there was little overall decrease in the average harvest (Fig. 7).

Figure 6
Annual guano production from Bird Island, Lamberts Bay off the west coast of South Africa (smoothed by threes) and the biomass of 0-year-old South African pilchard, 1950–76. From Crawford and Shelton (1978)

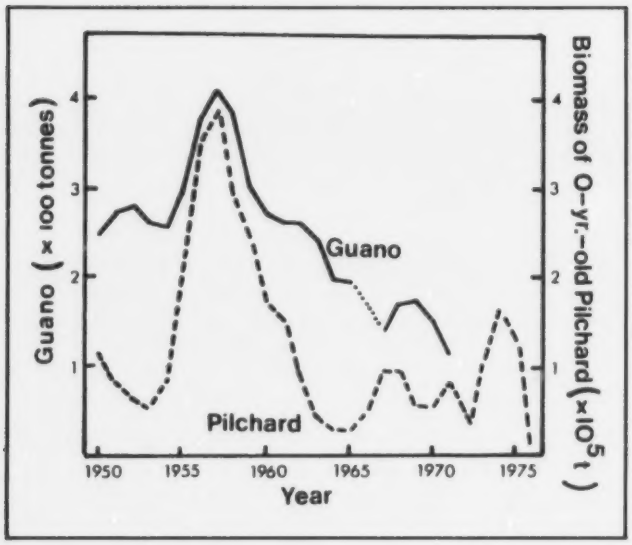
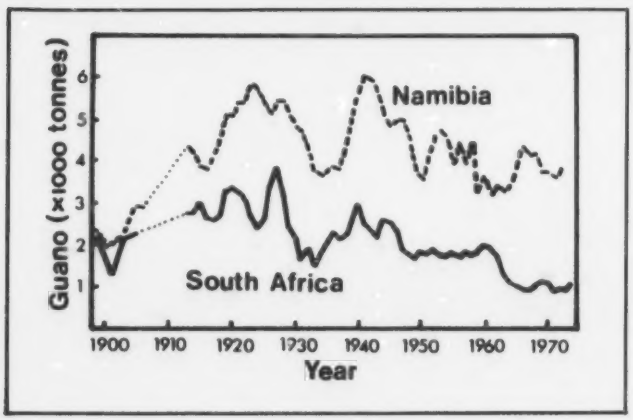


Figure 7
Guano production on all islands situated off South Africa and Namibia, excluding the guano platforms (smoothed by threes). From Crawford and Shelton (1978) with additional data from Newman and Crawford (1979)



7. Dietary changes in the seabirds

Analyses of the diets of Cape Gannets, Jackass Penguins, and Cape Cormorants on the west coast of South Africa and in Namibia are shown in Tables 2 and 3. These data show the percentage relative abundance of items in the stomach contents. Analyses of the percentage mass of prey items in stomach contents show the same trends (Crawford and Shelton 1978, 1981; Cooper 1984; Furness and Cooper 1982). Dietary changes between the mid 1950s and 1977–80 show the effects of the very intensive purse-seine fishing between these periods.

The larger-sized shoaling fish, notably pilchards and horse mackerel, which were very important prey for all three seabird species in the 1950s, became absent or much reduced in the diets of the birds (Tables 2 and 3). This trend correlated with the decrease in landings of pilchards and horse mackerel by purse seiners (Figs. 2 and 3). In 1977–80, anchovies were the main food resource for all three seabird species on the west coast of South Africa, and for Cape Gannets in Namibia. Round-herring increased in importance in the diets of the penguin and the Cape Cormorant. The increase of pelagic gobies in the diets of Jackass Penguins and Cape Cormorants breeding north of Lüderitz, Namibia possibly indicates an increase in the stocks of this fish in a localized area (Cruickshank *et al.* 1980). The penguins breeding on the islands just south of Lüderitz did not eat gobies to the same extent in 1980 (Table 3).

Despite changes in the species composition of their diets, between the 1950s and 1977–80, the Jackass Penguin and Cape Cormorant continued to feed predominantly on the pelagic shoaling fish. These birds possess anatomical and behavioural adaptations for exploiting this type of prey (Siegfried *et al.* 1975*a*, 1975*b*; Burger 1978). The Cape Gannets on the west coast of South Africa have shown a shift in their diet to include more non-shoaling fish species, and to include demersal hake scavenged from the deep-sea trawlers (Cooper 1984).

Batchelor (1982) made an intensive study from 1978 to 1981 of the diet of Cape Gannets breeding on Bird Island, Algoa Bay on the east coast of South Africa. He found that pilchards were the most common prey, comprising 44.4% of the numerical frequency of items in regurgitations, with anchovy (34.0%) and sauries (*Scomberesox saurus*) (14.0%) also common. Scavenging of demersal fish from trawlers was also evident but was apparently not as frequent as found by Cooper (1984) for gannets on the west coast. There are no data from Algoa Bay from earlier years with which to compare Batchelor's (1982) data. Batchelor found during the 4 years of study that pilchards became less important, and anchovies and sauries more important in the gannets' diet.

8. Discussion

There have been major changes in the populations of pelagic fish species off southern Africa during the past three decades. Fisheries biologists have attributed these changes to overexploitation of certain stocks by purse-seiners (Crawford and Shelton 1978, Newman and Crawford 1979), although this might have accentuated naturally occurring population fluctuations (Crawford and Shelton 1978). Although the fisheries have had reduced harvests, it is difficult to assess whether there has been an overall

decrease in the quantities of fish available to seabirds in southern Africa. The available evidence is inadequate and contradictory.

Analyses of catch statistics indicated that the combined abundance of all commercially important pelagic fish species in South Africa declined by 60–70% since 1960 (Newman and Crawford 1979). The guano data have been interpreted as indicating a 50% reduction in availability of fish to seabirds in the same interval (Newman and Crawford 1979). By contrast, censuses of breeding birds indicate an increase in abundance of seabirds between 1956 and 1978 in South Africa (Table 2). In Namibia, despite declining landings by fishermen, the guano harvests did not decrease significantly. Populations of Cape Cormorants in Namibia were greater in 1978 than they were in 1956, although this was probably due to the increased availability of nest sites on guano platforms. Clearly the factors affecting seabirds are not identical to factors affecting fishing harvests, and continued monitoring of the populations and diets of seabirds in specific regions is needed.

The cause for concern is perhaps not that there might be fewer pelagic fish, of all species, now available to seabirds but that certain important changes have occurred which have affected seabirds: there are now fewer pilchards and horse mackerel available; there are fewer large fish available, of any pelagic shoaling species. Pilchards were the most frequent prey of Cape Gannets, Cape Cormorants, and Jackass Penguins in 1956 and the depletion of the stocks of adult pilchards on the west coast of South Africa and off Namibia has had major consequences for these birds. It is significant that Crawford and Shelton (1978) found correlations between local pilchard abundance and guano harvests at several localities in these regions. Horse mackerel were important in the diets of these seabirds off South Africa in 1956, but following the drastic reduction of this fish in purse-seine catches, were negligible in their diets in 1977–79. Cape Gannets, Jackass Penguins, and Cape Cormorants have all shown capability of switching prey species, when pilchards and horse mackerel were apparently less available, but they have not been equally successful at adapting to the changes.

The decrease in the population of Cape Gannets off Namibia seems to be associated with the reduced availability of pilchards. The decrease was perhaps mediated by the availability of anchovies, although the greatest concentrations of anchovies are not close to the gannetries (Crawford and Shelton 1981). The gannet populations on the west coast of South Africa have remained fairly stable and pilchards and horse mackerel have been replaced in their diets by anchovies, non-shoaling pelagic fish and hake taken from demersal trawlers (Cooper 1984). The gannet has a greater foraging range and a larger gape than the penguin and the Cape Cormorant, and appears better suited to scavenging the large fish available at the offshore

Table 2
Changes in the diets of Cape Gannets, Jackass Penguins, and Cape Cormorants in the southwestern Cape coast, South Africa. The species composition of the birds' diets is expressed as percentage relative abundance of items in the stomach contents

	Cape Gannet					Jackass Penguin			Cape Cormorant			
Sample period:	**1953–54**	**1954–55**	**1954–56**	**1978–79**	**1977–78**	**1953–54**	**1954–55**	**1977–78**	**1953–54**	**1954–55**	**1954–56**	**1977–78**
Source of data:	**Davies (1955)**	**Davies (1956)**	**Rand (1959)**	**Crawford and Shelton (1981)**	**Cooper (1984)**	**Davies (1955)**	**Davies (1956)**	**Cooper (1984)**	**Davies (1955)**	**Davies (1956)**	**Rand (1960b)**	**Cooper (1984)**
Pilchard	44	62	19	2	13	37	49	1	36	44	15	5
Anchovy	30	26	25	78	39	2	44	84	32	19	12	50
Horse mackerel	18	11	30	1	1	23	2	0	21	14	16	1
Round herring	0	0	1	3	1	0	0	14	0	0	3	25
Mackerel	6	0	4	0	1	20	2	0	0	0	1	0
Other fish, crustaceans, and cephalopods	1	1	21	16	45	18	3	1	12	23	54	19
No. of birds examined	98	191	257	1224	203	16	112	30	37	77	204	119

Table 3
Changes in the diets of Cape Gannets, Jackass Penguins, and Cape Cormorants in Namibia. The species composition of the birds' diets is expressed as relative abundance of items in stomach contents

	Cape Gannet		Jackass Penguin			Cape Cormorant	
Sample period:	**1957–58**	**1978–79**	**1957–58**	**1980***	**1980†**	**1957–58**	**1978–79**
Source of data:	**Matthews (1961)**	**Crawford and Shelton (1981)**	**Matthews (1961)**	**Crawford and Shelton (1981)**	**Crawford and Shelton (1981)**	**Matthews (1961)**	**Crawford and Shelton (1981)**
Pilchard	85	1	83	0	0	76	0
Anchovy	0	85	0	0	21	0	28
Horse mackerel	10	0	6	0	0	18	1
Pelagic goby	0	5	0	92	17	0	65
Other fish, crustaceans, and cephalopods	5	8	11	9	61	5	6
No. of birds examined	155	256	19	121	83	210	176

*From Mercury and Ichaboe islands, north of Lüderitz.
†From Halifax and Possession islands, south of Lüderitz.

trawlers. The increase in the gannet colony at Algoa Bay was perhaps due to the availability of pilchards there. Pilchards were the most important prey of these gannets in 1978–81 (Batchelor 1982) and Crawford (1981*a*) has shown that there might still be seasonally abundant stocks of pilchard on the south and east coasts. Pilchards were very common in the stomach contents of hake caught near Algoa Bay but not in hake off the west coast (Crawford 1981*a*).

Jackass Penguins have almost certainly been adversely affected by the purse-seine fishery. The greatest concentrations of the penguins are on the west coast of South Africa and Namibia, where there has been the most intensive fishing and where stocks of the penguins' preferred prey have been depleted. The population of penguins has decreased alarmingly, despite the abundance of anchovies in some areas (Crawford 1981*b*). By contrast, penguin populations have increased on the south and east coasts, where there are stocks of 2–4-year-old pilchards (Crawford 1981*a*). Jackass Penguins are thought to require predictable shoals of prey close to their breeding colonies, because of their restricted foraging range (Frost *et al.* 1976). Pilchards have a predictable temporal and spatial distribution, and are therefore probably better suited to the penguins than the less predictable anchovies (Crawford 1981*a*, 1981*b*). Jackass Penguins at two islands off Namibia appear to be successfully exploiting pelagic gobies, but further investigation is needed to determine whether this fish will continue to support the penguin population.

Crawford and Shelton (1978) speculated that the increase in the population of Jackass Penguins at Dyer Island might be due to immigration from the west coast. This requires confirmation. Such movements to favourable feeding areas could be an important adaptation for overcoming variability of the food resource. The Jackass Penguin is regarded as a threatened species (Frost *et al.* 1976). Its population and diet are being monitored at a few colonies. These activities need to continue and expand and several of the research priorities outlined by Frost *et al.* (1976) still require attention.

The recent changes in the pelagic fish populations have apparently affected the Cape Cormorant less than the gannet and the penguin (Crawford and Shelton 1981, Cooper *et al.* 1982). These cormorants are the smallest of these species, and perhaps better adapted to feeding profitably on the smaller shoaling fish. Crawford and Shelton (1981) showed that aspects of the breeding biology of the Cape Cormorant are well adapted to exploiting variable food resources and moving into colonies near available food supplies. Off South Africa these cormorants have successfully exploited the available anchovies and round herring, and their numbers have increased. The very large increase of the Dyer Island colony might be related to the availability of pilchard there. Off Namibia, the censuses and records of guano harvests at the platforms show that the population of Cape Cormorants increased when additional breeding space became available in the 1960s, but that the population decline that followed coincided with reductions in the pilchard biomass (Crawford and Shelton 1981, Cooper *et al.* 1982).

Although there has been no apparent adverse effect of the fishing industry on the overall population of Cape Cormorants, Cooper *et al.* (1982) have warned that overexploitation of anchovies and other pelagic fish could lead to drastic decreases in Cape Cormorant numbers.

Reductions of pilchard populations probably meant a reduction in the quality of fish available to seabirds off southern Africa. Batchelor (1982) showed that the energy content and concentrations of protein and fat were higher in pilchards than in anchovies, sauries, horse mackerel, hake (*Merluccius capensis*), and squid. Batchelor (1982) found that Cape Gannet chicks experimentally fed on pilchards had higher assimilation efficiencies, growth rates, and maximum weights than chicks fed on hake. Further experiments are required to test the effects of fish quality on breeding success in South African seabirds.

Fisheries biologists in southern Africa have recently begun to monitor population changes and breeding success in selected seabird species, to assess their use as indicators of available fish stocks (Newman and Crawford 1979; P.A. Shelton, pers. comm.). The underlying assumption is that food availability is the ultimate limiting factor for these populations. This might not always have been the case and we present a series of graphical models, showing how human interference might have altered seabird populations and the factors limiting them (Fig. 8).

We suggest that, prior to the arrival of European settlers, 330 years ago, the overall population of all seabirds in southern Africa was limited by the availability of nest sites. All major seabird colonies were on small offshore islands. The breeding success and densities of birds on each island might have been restricted by the availability of food within the foraging range of the breeding adults, and hence fluctuations in local fish populations might have caused fluctuations in guano deposits, as seen recently on some islands. But the lack of suitable islands near some of the richest foraging areas, particularly off Namibia, probably limited overall numbers. An analogous situation is found off the coast of Senegal, where despite high marine productivity there are few seabirds. This is possibly a consequence of a lack of suitable nesting habitat (Brown 1979). Under these conditions, fluctuations of fish populations in time and space might seldom have had major effects on total seabird numbers (Fig. 8*a*).

Human disturbance reduced the availability of suitable nesting habitat. The exploitation of eggs and guano led to the extinction of some seabird colonies and the reduction of others (Westphal and Rowan 1971, Frost *et al.* 1976, Shaughnessy and Shaughnessy 1978). These disturbances might have reduced overall numbers of seabirds (Fig. 8*b*).

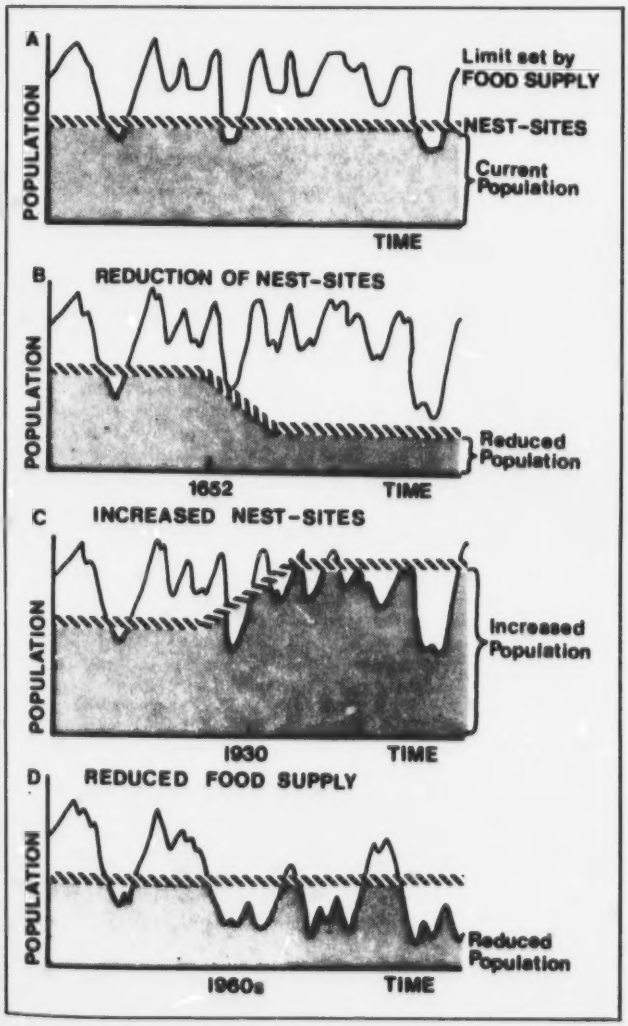
The construction of the huge guano platforms in the 1930s and 1960s at Walvis Bay, Cape Cross, and Swakopmund (Berry 1975, Crawford and Shelton 1981) increased the availability of nesting habitat in the proximity of the very productive sea off Namibia. There have been over 500 000 Cape Cormorants breeding or roosting on these platforms (Berry 1976*a*), where previously there had been no natural offshore islands. Some Cape Cormorants and Great White Pelicans had previously been using a few temporary sandy islands in coastal lagoons (Crawford *et al.* 1981, Cooper *et al.* 1982). The overall population of seabirds probably increased at this time (Fig. 8*c*).

Following the reduction of certain populations of pelagic shoaling fish by purse seiners, it now seems probable that food is limiting seabird populations in many areas of southern Africa (Fig. 8*d*). Direct censuses plus analysis of guano harvests have shown that numbers at some seabird colonies seem to be correlated with the abundance of certain local fish stocks, notably those of pilchards (Crawford and Shelton 1978, 1981; Cooper 1984). This trend is not always

apparent because some seabird species have shown greater resilience to change than others. Reductions in large populations of seabirds have been found in ecologically similar coastal areas of Peru, California, and elsewhere, following intensive commercial fishing of shoaling fish (Jordan 1967, Idyll 1973, Ainley and Lewis 1974, and these proceedings).

There have been few attempts to relate apparent reductions of fish to poor breeding success in seabirds in southern Africa. High chick mortality, nest-desertion, and reduced breeding success of Cape Cormorants at several colonies have been attributed to low food availability (Berry 1976*a*, Crawford *et al.* 1980), but Rand (1960*b*) noted similar events in years before there was evidence of overfishing.

Figure 8
Factors possibly limiting populations of seabirds in southern Africa. A — Populations limited by the availability of suitable nesting sites. This situation might have occurred prior to the settling of Europeans in South Africa and Namibia, and might still apply to certain regions. B — Since the arrival of Europeans in the 17th century, exploitation and disturbance reduced the availability of undisturbed nest sites, possibly resulting in a population decline. C — The availability of nest sites increased with construction of guano platforms and the population of Cape Cormorants and some other species probably increased and might have become limited by food. D — Following a reduction in food availability related to intensive fishing, seabird populations were limited by food, not nest sites; the overall population size decreased and fluctuated with changing fish stocks. This situation probably prevails in many regions of South Africa and Namibia



It is a healthy sign that fisheries biologists have begun to include seabirds in their management plans. A greater knowledge of the responses by seabirds to changes in the availability of their prey is essential for seabird conservation and in the use of seabirds to monitor fish stocks. In particular it is essential to determine the factors limiting seabird populations at specific colonies, and the adaptability of each species for using alternative food resources. The effects on seabirds of changing fishing activities, such as the possible development of a pelagic goby harvest, would need to be monitored. Clearly seabird conservation and fisheries management are interlinked, and it is a welcome sign that the South African Government's Sea Fisheries Institute has recently appointed its first permanent seabird ornithologist.

9. Acknowledgements

We thank Robert Crawford, Robert Furness, and Peter Shelton for access to unpublished manuscripts and for constructive criticism of this paper. Ronald Abrams kindly gave us information. A.B. thanks Elizabeth Behrens, librarian at the Sir Wilfred Grenfell College for her considerable assistance. J.C. thanks the South African Nature Foundation for financial support towards research on Jackass Penguins.

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Seabird–fisheries relationships in the northeast Atlantic and North Sea

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1. Abstract

Bioenergetics modelling indicated that seabirds consume 29% of pelagic fish production within a 45-km radius of one Shetland colony. Assuming this is typical, it implies that seabirds, predatory fish, and industrial fisheries are in direct competition. Overfishing of whitefish stocks in the North Sea began in the 1880s and, coupled with more recent reductions of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) stocks, led to an increase in populations of small food-fish, particularly sandlance (*Ammodytes marinus*). Most seabird species have increased in numbers in Scotland since 1900, probably in response to the increased availability of food resulting from these ecosystem changes. Rates of increase have been higher in areas where sandlance have become most abundant. Seabirds breeding in Shetland feed mainly on sandlance and have increased many times faster than the populations of the same species on St. Kilda, an area where fishing pressures have been much lower and seabird diets are more varied. Large scavenging species in Shetland, particularly Herring Gulls (*Larus argentatus*), Skuas (*Catharacta skua*), and Northern Fulmars (*Fulmaris glacialis*), are dependent on refuse from whitefish boats. Current trends to reduce volumes of whitefish discarding and increase industrial fishing for sandlance are likely to reduce food availability to seabirds. Monitoring will be necessary to determine which aspects of life history are affected by this.

2. Résumé

La technique de modélisation bioénergétique révèle que les oiseaux de mer consomment 29 % de la production de poissons pélagiques dans un rayon de 45 km d'une colonie de l'île Shetland. En supposant que ce modèle soit typique, cela veut dire que les oiseaux de mer, les poissons prédateurs et la pêche commerciale sont en concurrence directe. La surexploitation des stocks de corégone dans la mer du Nord a commencé dans les années 1880 et, conjuguée aux réductions plus récentes des stocks de hareng (*Clupea harengus*) et de maquereau (*Scomber scombrus*), a donné lieu à un accroissement des populations de petits poissons-fourrages, en particulier celle du lançon (*Ammodytes marinus*). La plupart des espèces d'oiseaux de mer ont vu leur nombre augmenter en Écosse depuis 1900, probablement à cause d'une plus grande disponibilité de nourriture résultant de ces modifications d'écosystème. Les taux de prolifération ont été plus élevées dans les régions où le lançon est devenu plus abondant. Les oiseaux de mer qui nichent dans l'île Shetland se nourrissent principalement de lançons et se sont multipliés beaucoup plus rapidement que les populations de la même espèce vivant dans l'île St. Kilda, région où la pression de la pêche a été beaucoup plus faible et où le régime alimentaire des oiseaux de mer est plus varié. Les espèces de charognards de l'île Shetland, en particulier le Goéland argenté (*Larus argentatus*), le Grand Labbe (*Catharacta skua*) et le Fulmar boréal (*Fulmaris glacialis*) dépendent des rejets provenant des bateaux de pêche au corégone. Les tendances actuelles visant à réduire les volumes de rejets de corégone et à intensifier la pêche industrielle au lançon sont de nature à réduire la disponibilité de nourriture pour les oiseaux de mer. Il faudra exercer une certaine surveillance pour déterminer quelles étapes du cycle biologique des oiseaux sont touchées par ces changements.

3. Introduction

Increased competition between nations for fish catches in the northeast Atlantic has led to concern that top predators, such as seals and seabirds, remove large quantities of fish which would otherwise provide an economic profit for fishermen. Conversely, the increasingly intense exploitation of fish stocks may lead to changes in the marine ecosystem which adversely affect the seabird and seal populations we would wish to conserve.

The North Sea and the northeast Atlantic over the continental shelf provide one of the richest yields of fish in the world. Detailed data on catches, fishing effort, and stock size and composition have been collected for commercial fish species since the creation of the International Council for the Exploration of the Seas (ICES) in 1899. The long history of its exploitation is well recorded (Graham 1956, Hardy 1959, Lundbeck 1962, Hempel 1978*a*) and was the subject of a symposium on the causes of changes in fish stocks (Hempel 1978*b*). The structure and productivity of the North Sea marine ecosystem has also been investigated in considerable detail (Steele 1974).

The British Isles, and particularly Scotland, hold large breeding populations of seabirds. Changes in the sizes of these seabird populations have been documented for many species in many colonies and provide an opportunity to examine correlations between changes in seabird and fish populations over a long time period. In this paper I shall briefly review the evidence that seabirds are a major predator of pelagic fish and in competition with fisheries and predatory fish. I shall then outline the changes in fish stocks around Scotland since the end of the 19th century, and present data indicating the responses shown to these changes by breeding seabird populations. This will provide

the framework for some tentative predictions concerning the future influences of commercial fishery practices on seabird populations.

4. Fish consumption by seabirds

I have discussed the use of bioenergetics modelling in estimating the food consumption by seabirds (Furness, this volume). Application of this approach to one of the largest seabird communities in the British Isles (Furness 1981) suggested that the seabirds consume 29% of the annual pelagic fish production from the sea area within 45 km of the colony, on Foula, Shetland (Furness 1978). Similar values have been obtained in a number of different studies (e.g. Wiens and Scott 1975, Furness and Cooper 1982). Four species on Foula, Northern Fulmar (*Fulmarus glacialis*), Common Murre (*Uria aalge*), Shag (*Phalacrocorax aristotelis*), and Atlantic Puffin (*Fratercula arctica*) are responsible for 90% of the annual total energy requirements of the 18-species community, so the accuracy of calculations for these species determines the overall accuracy of the estimate for the community. Each of these species in Shetland feed their chicks almost exclusively on small pelagic fish, principally sandlance (*Ammodytes marinus*). However, diets of breeding and non-breeding seabirds may differ from each other, and from that fed to chicks (Furness and Hislop 1981). In particular, offal may make an important contribution to the requirements of adult, particularly non-breeding, Northern Fulmars so reducing their consumption of pelagic fish. This is not true for the other three species, though marine invertebrates may occur in the diet of non-breeding alcids. At present there are no quantitative data to indicate the importance of these two foods.

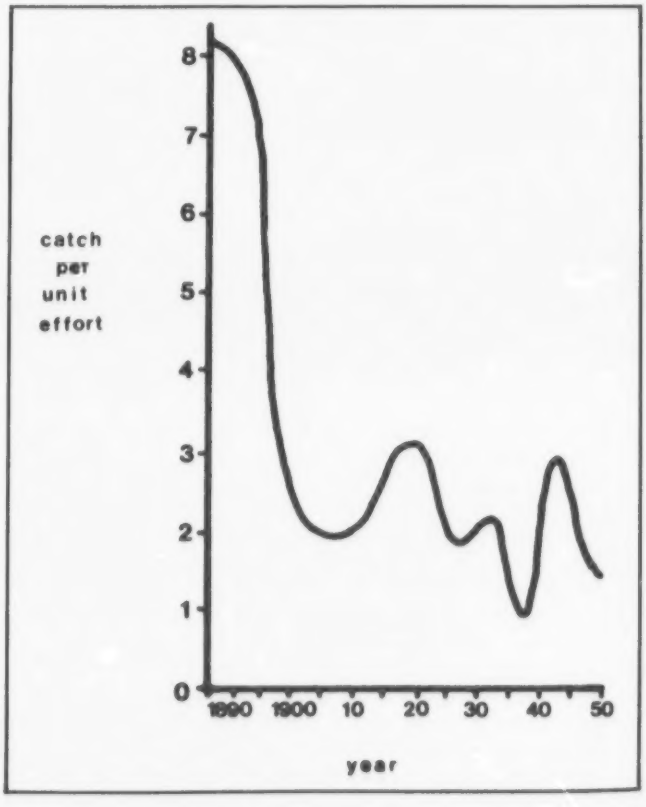
The second serious difficulty in relating population energy requirement to fish production stems from uncertainties in the range over which the seabirds forage. Transect counts near colonies show high concentrations of seabirds close to the colony and a low, patchy distribution at considerable distances, but it is unclear whether these are foraging breeders or immatures. However, they do indicate that in most situations around British colonies, Shags feed within a few kilometres of the colony, alcids travel a few hundreds of metres to a few tens of kilometres, and Northern Fulmars appear to spread themselves rather uniformly over at least 50 km from the colony. Dye-marking Northern Fulmars feeding chicks on Foula resulted in reports from fishermen who saw these individuals at sea. Most were reported from within 50 km; the few records from further afield could have been birds that deserted their nest as a direct result of being caught and dye-marked, since 20% of the birds marked were never seen at their nests again (Furness and Todd, in press). An index of the maximum foraging range can be obtained from the time spent away from the nest between chick feeds (Pearson 1968). These indicate that Atlantic Puffins, Common Murres, and Shags feed close to the colony, whereas Northern Fulmars depart for longer. Half the departures recorded at Foula by adult Northern Fulmars with chicks lasted for less than 6 h. If these birds flew in a straight line at 40 km/h they would have travelled no more than 120 km from the colony (Furness and Todd, in press). In practice, as feeding takes time, and flight is unlikely to be direct, their ranges were smaller than this. The main Shetland seabird communities are about 70 km apart, and placed at the corners of the archipelago. Birds travelling more than 35 km may enter the feeding zone of the adjacent colony, so to some extent will compensate for others travelling in the opposite direction. The estimate that all feeding occurs over a 45 km range from the colony seems a reasonable compromise given these uncertainties (see also Blake *et al.* 1980).

Steele (1974) indicated that, on average, 50% of pelagic fish production in the North Sea is taken by people. If the seabirds consume 29%, then 21% remains to be shared by marine mammals, and demersal and other predatory fish, indicating that the relationship between seabird consumption, pelagic fisheries, and predatory fish is tight, with little scope for an increase in one without a concomitant decrease in another.

5. Changes in fish stocks

The introduction of steam trawling and power winches between 1870 and 1900, together with the development of the otter trawl towards the end of the 19th century, greatly increased fishing power. Lundbeck (1959, 1960, 1962) showed that a severe reduction in whitefish biomass occurred almost immediately, particularly in the southern North Sea (Fig. 1) where stock biomass was reduced by 70% at the turn of the century. He attributed this to overfishing as a result of increased effort, and this interpretation is supported by the tendency for the stock to show temporary increases during the two world wars (1914–18 and 1939–45) when fishing effort was much reduced. Thus a major

Figure 1
Catch per unit effort of a standardized German trawler in the southern North Sea (Lundbeck 1962) showing effects of increased fishing on fish stock size: all whitefish species combined



reduction in whitefish stock biomass took place around 1890 to 1900, just when the exploitation of seabird populations by people was also tending to cease. The increase of many seabird populations dates from about 1900, suggesting that it could be a response to the reduced predation on "food-fish" by whitefish, making more food available to the seabirds. Protection of seabirds may have accelerated this process, but it seems likely that the increased food availability would have been necessary to allow most populations, except those reduced near to extinction, to increase.

Whitefish also responded to the improved food availability as a result of stock reduction. Haddock (*Melanogrammus aeglefinus*) growth rate increased (Jones and Hislop 1978) as did that of whiting (*Merlangius merlangus*) (Daan 1975). As a result of increased growth rates both species reached reproductive condition at an earlier age. Cod (*Gadus morhua*) showed no change in growth rate, but the age of maturity did decrease so that cod reached reproductive age at a smaller size (Daan 1978). All these changes may be ascribed to greater food availability per fish as a result of reduced competition.

Depletion of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) stocks in the North Sea and northeast Atlantic had begun before 1950, but was greatly accelerated by the introduction of purse-seining. The adult biomass of North Sea herring remained around 2.5×10^6 t until 1965 when it was depleted in a few years to one-tenth of this. At the same time, the growth rate increased suddenly, and partly compensated for the reduction in stock (Burd 1978). When herring became unprofitable the purse-seine fishery turned to mackerel. The stock of 2×10^6 t before 1965 was reduced to about one-tenth of this in only 4 years of fishing (Hamre 1978). The fisheries for adult herring and mackerel before 1960 will have been directly beneficial to seabirds by reducing the average size of fish in the populations without greatly reducing stock biomass, so that a higher proportion of the stock will have been in the size range suitable for seabird consumption. After 1960 the reductions in stocks will not have been directly beneficial to seabirds, but as most species feed more on sandlance than on herring or mackerel there was probably an indirect beneficial effect.

Andersen and Ursin (1977) found that the reduction in stocks of herring and mackerel is likely to have led to increases in the populations of their ecological competitors: sandlance, sprats (*Sprattus sprattus*), and Norway pout (*Trisopterus esmarkii*). Evidence that such increases have taken place is not readily available as sandlance were of no commercial interest until recently; so stock sizes were, and still are, largely unknown. However, Sherman *et al.* (1981) have shown that there is good evidence for a large increase in sandlance stocks in the northeast and northwest Atlantic. Catch per unit effort of Norway pout by Scottish research vessels shows that the stock of this species has also greatly increased since the mid 1950s from a level which had previously been fairly constant (Richards *et al.* 1978).

Andersen and Ursin's model also predicted that whitefish stocks would increase as a result of decreased predation on their larvae by herring and mackerel. Such increases have occurred, and are very difficult to explain except in terms of such an ecosystem interaction (Hempel 1978*a*). As a corollary of their recovery the growth rates of whitefish have fallen again, which suggests that the super-abundance of food generated by their stock depletion no longer exists (Hempel 1978*a*).

The reduction of herring and mackerel stocks will have been beneficial to seabirds in allowing an increase in their main food, sandlance, although the partial recovery of whitefish stocks will have increased predation on adult sandlance. A result of these ecosystem changes has been a rapid growth of industrial fishing for sandlance (and sprats and Norway pout) since its inception in the 1950s. In the 1970s total landings of industrial fisheries in the North Sea exceeded landings of whitefish, averaging over 2 million metric tons/year (Fig. 2). Sandlance catches are continuing to increase rapidly (Fig. 3), although little is known of the stock size or maximum sustainable yield for this species, so that fishing effort is likely to continue to be increased until the stock suffers fishery-induced reduction in size and yield.

Figure 2
Total landings of industrial fisheries in the North Sea (from Popp Madsen in Hempel 1978*a*)

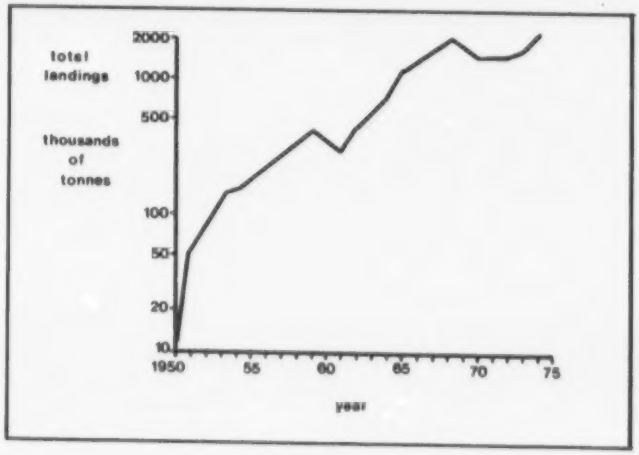
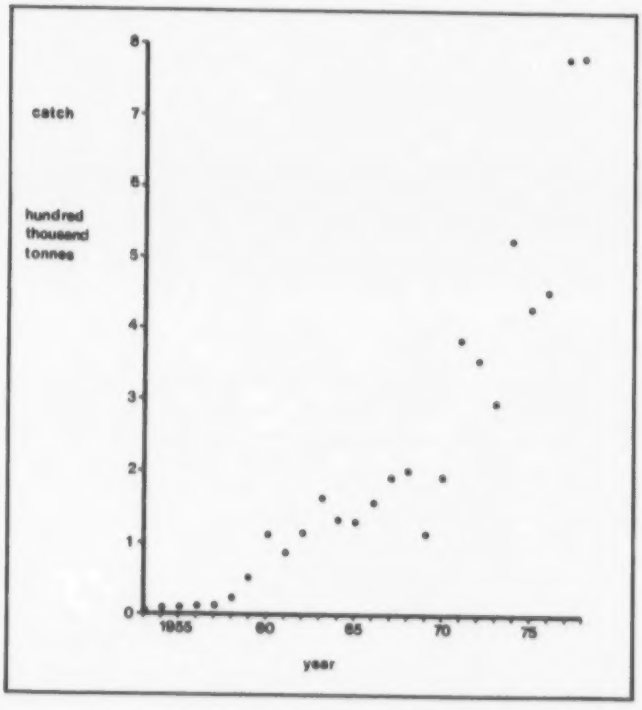


Figure 3
Annual catches of sandlance in the North Sea (from K. Warburton, pers. comm.)



The total annual landings of whitefish from the North Sea remained around 0.5 million metric tons from 1910 to 1960, then increased to slightly over 1 million metric tons after 1965, as a consequence of enhanced recruitment which may have been a response to decreased predation on whitefish larvae by the depleted herring and mackerel stocks (Hempel 1978*a*). Legal restrictions on the minimum sizes of fish that can be marketed, and fluctuations in market demand and catch quotas, result in a proportion of each catch being discarded, mainly dead, into the sea. This proportion has increased with the reduction in average fish size; now a higher proportion of the population is caught as soon as it is recruited into the fishable stock. Up to 30% of a whitefish catch in the North Sea may now be discarded at sea (Jermyn and Hall 1978). Discard fish, and offal, which is probably equal in weight to the amount of discards (Bailey and Hislop 1978), provide a source of food for Northern Fulmars, large gulls, Skuas (*Catharacta skua*), Northern Gannets (*Morus bassanus*), and Black-legged Kittiwakes (*Rissa tridactyla*). The yield of whitefish to commercial fisheries in the North Sea could be increased in the long term by increasing minimum net-mesh size, allowing smaller fish to escape and continue their growth until capture at a later date. Offal may be used to supplement industrial fish catches for reduction purposes, so that quantities thrown away may be reduced in future. Discarding undersized fish is also wasteful, though difficult to avoid with present fisheries management. Increased net-mesh size, or limited entry to fisheries through a licensing scheme have been suggested as conservation measures (Gulland 1982). These, or temporary closure of fisheries when quotas have been met, would further reduce food availability to seabirds.

6. Changes in seabird population sizes

Detailed surveys of breeding seabirds in Britain and Ireland have provided accurate information on the sizes and rates of increase of populations of many species. Most seabird populations in Scotland have been increasing for the last 80 years or so. Rates of increase have probably been highest in the gulls, stercorarids (Skua and Parasitic Jaeger *Stercorarius parasiticus*), and Northern Fulmar. For many species they have been highest in east Scotland and lowest in west Scotland (Table 1). These population changes are reviewed by Cramp *et al.* (1974), Harris (1976*a*, 1976*b*), Harris and Galbraith (1983), Harris and Murray (1978), and Furness (1982).

7. Regional differences in seabird diets and foraging

Seabirds can be classified into four major foraging guilds: zooplankton, trawler-waste, small pelagic fish, and

Table 1
Rates of change (percent per annum) of seabird population sizes at St. Kilda, Shetland, and east Britain. Data from Cramp *et al.* (1974), da Prato and da Prato (1980), Furness (1977, 1981), Harris (1976*a*, 1976*b*), Harris and Galbraith (1983), Harris and Murray (1978), Hawkey and Hickling (1981), Murray (1981), and Nelson (1978). Values quoted are average rates to nearest 1% over periods where the rate appears to have been constant

	West coast	Shetland			East coast		
Species	St. Kilda (57°48′N 8°35′W)	Foula (60°08′N 2°05′W)	Hermaness (60°52′N 0°54′W)	Noss (60°08′N 1°00′W)	Isle of May (56°10′N 2°32′W)	Berwickshire (55°55′N 2°10′W)	Farnes (55°38′N 1°36′W)
Northern Fulmar	1900–70 +1% 1970–80 0	1878–1976 +8%	1910–74 + 6%	unknown	1930–81 + 6% 1975–81 +15%	1957–78 +4%	1972–80 +4%
Northern Gannet	1900–70 +2% 1970–80 0	absent	1939–69 +2.6%	1939–69 +2.8%	absent	absent	absent
Shag	1930–80 0	unknown	1965–70 +7%	little change	1950–73 +16% (1973–76) –38% 1978–81 +24%	1957–78 0	1955–71 +2% 1971–74 +23% (1974–75) –65% 1975–80 +19%
Skua	1900–60 absent 1960–80 +18%	1900–76 +7% 1976–81 –2%	1900–76 +5% 1976–81 0	1910–32 +15% 1955–81 +1%	absent	absent	absent
Lesser Black-backed Gull	1930–80 0	very few	very few	1946–74 –8%	1930–72 +13% 1972–81 controlled	1957–78 0	1972–74 +13% 1974–80 controlled
Herring Gull	1930–80 –2%	very few	little change	1946–73 0 1973–80 –10%	1907–72 +13% 1972–81 controlled	1957–80 0	1972–74 +13% 1974–80 controlled
Great Black-backed Gull	1930–80 0	1900–80 +4%	very few	1946–73 +2%	absent	absent	absent
Black-legged Kittiwake	1930–70 0	1900–61 increased 1961–76 0 1976–80 –3%	1965–74 +2%	unknown	1921–52 0 1954–81 +6%	1957–78 +5%	1972–80 +4%
Arctic Tern	absent	1906–80 increased	very few	very few	absent	absent	1956–80 0
Common Murre	1960–80 +3%	increasing	1960–79 increasing	increasing	1974–81 +5%	1957–78 +4%	1972–80 +18%
Razorbill	unknown	unknown	1965–74 +4%	unknown	1969–81 +16%	1957–78 +5%	1957–72 0 1972–79 +13%
Atlantic Puffin	1940–50 increased 1970–80 0	increasing	increasing	increasing	1959–81 +22%	1957–78 0	1972–79 +3%

predation–scavenging. The sizes and composition of these guilds vary between areas (Table 2). In particular, at St. Kilda zooplankton feeding is most common, in Shetland most species are members of the small pelagic fish-feeding guild as sandlance is the staple diet of most seabirds in the area, and in east Scotland (specifically around colonies off the Fife and Lothian coast) zooplankton is of negligible importance during the breeding season but trawler-waste and small pelagic fish are both important (Table 2). Quantitative studies of seabird diets around Britain are rather few. I have examined the diets of Northern Fulmars, Herring Gulls (*Larus argentatus*), and Skuas at St. Kilda (west Scotland) and Foula (Shetland), and the diets of Herring Gulls around the islands off the Fife–Lothian coast (east Scotland). Harris and Hislop (1978) have described the diets of young Atlantic Puffins from these same colonies.

Northern Fulmars on St. Kilda feed largely on zooplankton (Table 3) and have derived little benefit from the small local fishing industry. In Shetland their diet consists chiefly of sandlance caught at surface shoals and lesser quantities of offal and plankton (Table 3).

Gulls are known to be catholic in their feeding. Although subject to a number of potential biases (Furness and Hislop 1981) analysis of regurgitated pellets of indigestible material indicates that Herring Gulls on St. Kilda feed largely by scavenging or predating seabird eggs and young, scavenging intertidally and, to a small extent by kleptoparasitism of Atlantic Puffins and scavenging at trawlers (Table 4). On Foula, most of their diet consists of whitefish from trawlers, with small amounts of other items. At the Fife–Lothian colonies the diet consists almost entirely of food from human activities: whitefish discards, Norway lobster (*Nephrops norvegicus*) remains from trawlers, urban refuse, and earthworms from ploughed fields and pastures (Table 4).

In the Faeroe Islands the Skua feeds by piracy and predation of seabirds, and on goose-barnacles, squid, berries, and insects (Furness 1979, Furness and Hislop 1981). In Shetland it feeds mainly on sandlance, taking discard whitefish when sandlance are not readily available. As a result it has a reliable and high quality food supply, giving high breeding success (Furness and Hislop 1981). The diet of the small number of pairs that recently colonized St. Kilda is based on predation of seabirds and scavenging dead birds, goose-barnacles, and intertidal invertebrates and contrasts with the dependence of the species in Shetland on sandlance and discards (Table 5).

Atlantic Puffins at the Isle of May, east Scotland, have a higher chick growth rate and fledging weight than those at St. Kilda. The chick diet at the Isle of May consists mainly of sprats, whereas that at St. Kilda varies between seasons, but usually includes a large component of juvenile whitefish, which are of low calorific value (Harris and Hislop 1978). In Shetland, Atlantic Puffin diet is intermediate in calorific value, comprising almost exclusively sandlance, and chick growth rate is also intermediate (Furness, unpubl.).

Table 2
Feeding guilds of seabirds in three areas of the northeast Atlantic and North Sea coasts of Scotland: St. Kilda (west coast), Shetland (north coast), and Forth Islands (east coast). Species are classed as primary members if this is their principal feeding method, secondary if it is important but one of several methods used regularly, and tertiary if this is a minor source of food. Species: NF = Northern Fulmar, SP = Storm-Petrel, LP = Leach's Storm-Petrel, MS = Manx Shearwater, SH = Shag, NG = Northern Gannet, HG = Herring Gull, GG = Great Black-backed Gull, LG = Lesser Black-backed Gull, BK = Black-legged Kittiwake, S = Skua, PJ = Parasitic Jaeger, AT = Arctic Tern, CM = Common Murre, RZ = Razorbill, AP = Atlantic Puffin, BG = Black Guillemot

Guild	Area	Feeding level		
		Primary	Secondary	Tertiary
Zooplankton	St. Kilda	NF,SP,LP,MS	BK	CM,RZ,AP
	Shetland	SP,LP,MS		NF
	Forth Islands			NF,BK
Trawler-waste	St. Kilda	HG	GG	NF,MS,NG,S, BK
	Shetland	HG,GG	NF,S	NG
	Forth Islands	NF,HG,GG, LG	NG,BK	
Small pelagic fish	St. Kilda	NG,SH,CM, RZ,AP	MS,BK, BG	NF,SP,LP
	Shetland	NF,NG,SH,BK, S,PJ,AT,CM, RZ,AP,BG	SP,LP,MS, HG,GG	
	Forth Islands	NG,SH,CM,RZ, AP	BK	NF
Predation on birds/ mammals and scavenging at sea or on shore	St. Kilda	S,GG	HG	
	Shetland		S,GG	
	Forth Islands		GG	HG

Table 3
Diets of Northern Fulmars as indicated by presence (% occurrence) of ingested items in regurgitated samples from chicks and breeding adults collected between 1 June and 18 August 1978–81 (Furness, unpubl.)

Prey taxa	Foula, Shetland		St. Kilda, Hebrides	
	No. samples	%	No. samples	%
Sandlance	74	66	0	0
Sprats, herring	0	0	18	7
Fish offal	18	16	2	<1
Polystyrene	2	2	30	13
Paper, plastic, metal	3	3	8	3
Benthic invertebrates* (presumed trawl discards)	0	0	12	5
Pelagic zooplankton†	15	13	168	71
Total items sampled	112	100	238	100

**Munida bamffica, Pagurus bernhardus, Nephrops norvegicus, Liocarcinus tuberculatus, Acanthephyra* sp.
†*Meganyctiphanes norvegica, Gnathophausia zoea, Idotea metallica, Parapasiphara sulcatifrons.*

Table 4
Diets of Herring Gulls, expressed as % occurrence, as indicated by analysis of indigestible material in pellets (Furness, unpubl.)

Prey taxa	St. Kilda		Foula		Forth Islands	
	No. pellets	%	No. pellets	%	No. pellets	%
Sandlance	10	5	48	20	0	0
Sprats/herring	10	5	0	0	2	1
Whitefish	14	6	124	50	255	52
Nephrops norvegicus	0	0	0	0	89	18
Mytilus edulis	18	8	22	9	21	4
Earthworms	0	0	0	0	36	7
Crabs	11	5	14	6	16	3
Other shellfish	9	4	6	2	9	2
Domestic refuse	2	1	4	2	60	12
Eggshells	58	27	7	3	0	0
Seabirds	86	39	21	9	0	0
Total	218	100	246	100	488	100

Table 5
Diet (expressed as % occurrence) of breeding adult Skuas on St. Kilda, Hebrides, and Foula, Shetland, based on analysis of pellets (Furness and Hislop 1981; Furness, unpubl. data)

	St. Kilda, Hebrides		Foula, Shetland			
	1980	1981	1975	1976	1980	1981
Prey taxa	%(N = 82)	%(N = 50)	%(N = 560)	%(N = 386)	%(N = 100)	%(N = 100)
Sandlance	0	0	42	80	51	62
Whitefish	11	4	54	16	42	31
Birds/mammals	61	76	3	2	6	4
Littoral and marine floating invertebrates*	28	20	1	2	1	3

*Goose-barnacles (*Lepas* sp.), horse mussels (*Mytilus edulis*), and other invertebrates.

8. Competitive relationships between seabird species

The extent of interspecific competition between alcids and other species feeding on small pelagic fish is unknown. There is a clear linear dominance hierarchy in the guild feeding on trawler waste. Northern Fulmars displace all other species, but select offal and rarely attempt to take entire discard fish. Skuas can displace all species except Northern Fulmars. Northern Gannets dominate Great Black-backed Gulls (*Larus marinus*). Herring Gulls displace Lesser Black-backed Gulls (*Larus fuscus*) but are subordinate to the larger Great Black-backed Gulls. Black-legged Kittiwakes rarely attempt to join these associations in Shetland as they are unable to compete with any of the bigger birds, but in east Scotland, where there are relatively fewer Northern Fulmars and Great Black-backed Gulls and no Skuas, Black-legged Kittiwakes are occasionally found feeding at trawlers. Furness and Hislop (1981) found that Skuas in Shetland consumed up to 57% of the whitefish discarded by the fishing industry, depending on the availability of sandlance. The hierarchical arrangement suggests that when sandlance are scarce and skuas take a disproportionate share of the available discards the species low on the list are likely to suffer severe food shortage. For this reason the interspecific relationships may play an important role in the responses of seabird populations to changing fish stocks or fisheries practices.

9. Discussion

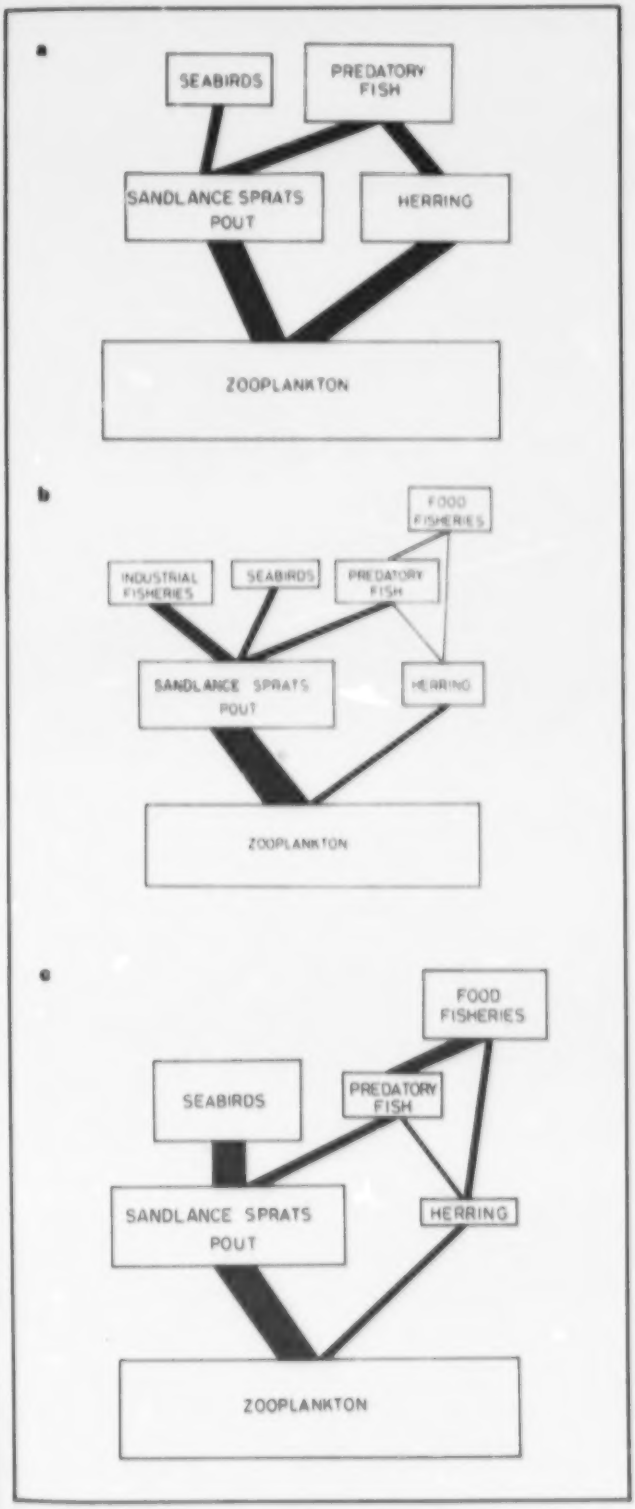
Seabirds have benefited from two quite distinct effects of North Sea fisheries. Firstly the provision of discards and offal has increased food available to scavenging species. Secondly, and of greater overall importance, ecosystem changes leading to expansion of sandlance stocks has increased food availability to almost all seabirds, as this fish is a major food for most seabirds in north and east Britain.

These changes can be summarized diagrammatically. Figure 4*a* shows the situation late in the 19th century. In Figure 4*b* the effects of reducing predatory fish and herring are indicated. Current, and likely future trends, to conserve whitefish and herring stocks and to increase industrial fishing on sandlance are seen as a threat to seabird populations (Fig. 4*c*).

Fishing intensity varies regionally. Off the west coast of Scotland whitefish catches have been rather small, and herring and mackerel stock depletion has only recently occurred. Comparisons of seabird diets in west, north, and east Scotland show that the seabirds on the east coast have altered their diets to take advantage of changes in food availability, whereas those on the west coast continue to utilize "traditional" prey. Rates of population growth mirror these dietary differences. On St. Kilda, the numbers of Northern Gannets, Common Murres, and Northern Fulmars have been increasing slowly; no change has been detected in recent years in numbers of Shags, Black-legged Kittiwakes, Lesser Black-backed Gulls, Great Black-backed Gulls, or Atlantic Puffins; and Herring Gull numbers have declined (Table 1). In Shetland, where sandlance stocks have increased and large quantities of whitefish discards and offal are available (Furness and Hislop 1981), increases have been measured in numbers of Northern Fulmars, Northern Gannets, Skuas, Black-legged Kittiwakes, Arctic Terns, Common Murres, and Atlantic Puffins. Herring Gulls and Lesser Black-backed Gulls have failed to show increases. East-coast colonies have shown a similar pattern to those in Shetland, except that gulls have also increased dramatically in this area, and rates of increase of several species have been higher than in Shetland, suggesting that changes in fish stocks have been most pronounced in this area, a conclusion supported by the fisheries data (Hempel 1978*a*, 1978*b*).

Northern Fulmars and Northern Gannets were subject to intense harvesting at St. Kilda up to shortly before the evacuation of the islands in 1931, yet their numbers have increased little since this chick mortality stopped. In other parts of Scotland both these species have shown rapid population increases. There appears to be no lack of potential but unused nesting space at St. Kilda. The failure of the St. Kilda populations to respond to relaxed predation is most easily explained by the populations being limited by food availability. This hypothesis is supported by the finding that the diet of Northern Fulmars at St. Kilda shows a negligible influence of fishery offal or increased availability of small pelagic fish, and so contrasts with the diets in the areas, such as Shetland, where the species is showing population increases. Unfortunately, little is known of Northern Gannet diets around Scotland. Atlantic Puffin numbers on St. Kilda are remaining approximately stable; numbers are increasing at eight other west-coast Scottish colonies, remaining constant at five and declining at two, whereas numbers in Shetland are increasing at eight colonies and stable at three. In east Britain all 10 colonies censused are increasing, at an average of 9% per annum (Harris 1976*a*; Harris and Galbraith, 1983). Again, rates of population change reflect changes in food availability induced by commercial fisheries around Scotland.

Figure 4
A diagram of energy flow from zooplankton to top predators in the North Sea ecosystem: (*a*) late 19th century, (*b*) in the 1960s when herring stocks were depleted, (*c*) probable picture for the 1980s with increased industrial fishing, conservation of herring and whitefish stocks, and possibly a decline in seabird populations as a result. Sizes of rectangles and widths of flow lines are intended to be indicative of magnitude although only for comparisons between stages *a*, *b*, and *c*. Scavenging species associated with commercial food fisheries are ignored for simplicity



Herring Gulls are uncommon and declining at St. Kilda, numerous but not increasing at Shetland, and numerous and increasing at 13% per annum at east-coast Scottish colonies (Cramp *et al.* 1974). Again, the rate of increase is highest in the area where human influences (in this case, not just fishing) are greatest.

Shags have shown the same regional differences; Potts (1969) argued that the density of breeding Shags on the east coast of Scotland was so low early in this century that it could not have been food-limited in a density-dependent manner. However, the rapid increase of Shag numbers on the east coast of Scotland, contrasting with their stable numbers on the west coast, is also compatible with the hypothesis that numbers have responded in areas where fishing has allowed sandlance and sprat stocks to increase.

By 1900 the Skua had been reduced by human persecution close to extinction: less than 20 pairs remained in each of the two Scottish colonies and the Faeroe Islands. After 1900 numbers increased in response to protection measures introduced in both countries (Cramp *et al.* 1974); in the Faeroes numbers stopped increasing at a population of around 500 pairs (Gibbs and Mawby 1968; Bloch, pers. comm.). Numbers in Scotland increased at 7% per annum to over 6000 pairs in 1976 (Furness 1977). Many individuals colour-banded as chicks in Shetland have emigrated to found new colonies in the Hebrides and north Scotland. Rates of increase are highest in these newly formed colonies which depend on immigration to sustain them. Skuas in Shetland are highly dependent on discard whitefish and sandlance, whereas the smaller populations in the Faeroes feed by more "traditional" methods: kleptoparasitism and predation. As the Skuas at St. Kilda also feed by predation and scavenging dead birds, goose-barnacles, and intertidal invertebrates, I would predict that the Skua colony on St. Kilda is unlikely to increase to a size comparable to those in Shetland, and that any reduction of sandlance or discard availability to Skuas in Shetland is likely to result in severe predation rates on other seabirds as the Skuas turn to their more characteristic feeding methods.

10. Conclusions

1. Shetland seabirds probably consume about 29% of annual pelagic fish production within a 45-km radius of the colony, implying that they are in competition with predatory fish and industrial fisheries.

2. Increases of seabird populations can be attributed to increased availability of food resulting from provision of offal and discards, and from increased stocks of sandlance caused by ecosystem changes attributable to intense commercial fishing.

3. Increases of seabird populations have been greatest in areas where ecosystem changes have been most marked. Diets vary between regions and indicate the opportunistic utilization of these increased food resources.

4. Future increases in fisheries for sandlance are likely to result in reduced seabird populations.

5. Reductions in the quantities of fish discarded would affect species low on the feeding hierarchy most severely.

11. Acknowledgements

I should like to thank J. Mauchline, J. Atkinson, and P.G. Moore for identifying invertebrates from Northern Fulmar regurgitates; M.P. Harris, the British Army, and the Nature Conservancy Council for logistical support on St. Kilda; D.N. Nettleship, J. Rice, and referees for helpful discussions and reviews of the manuscript.

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Capelin in the northwest Atlantic

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1. Abstract

Capelin (*Mallotus villosus*) is considered to be one of the most important fish species in the northwest Atlantic because of its commercial importance and its position as a forage species. Aspects of capelin biology including distribution, spawning, migration patterns, stock discrimination, population biology, and its position in the trophic structure of the northwest Atlantic are reviewed. The offshore commercial capelin fishery began in 1972, peaked in 1976, and has declined since then. The pattern of the commercial fishery and its management are reviewed. The status of capelin stocks has been determined by a surplus-production model, acoustic techniques, and analytical models; and the results of the analytical models indicated that the strong 1973 year-class resulted in relatively high capelin abundance in the mid 1970s. The 1974–78 year-classes were relatively weak and the capelin biomass declined during the late 1970s. Fishing mortality rates calculated from the analytical models have been low for stocks in Northwest Atlantic Fisheries Organization divisions 2J3K and 3L suggesting that fishing did not contribute significantly to the decline. Heavy fishing pressure on the division 3N0 stock may have exaggerated the decline of this stock. Factors influencing the dynamics of capelin populations and the possible effects of fluctuations of capelin on its predators are reviewed. The research program in capelin is presented.

2. Résumé

Le capelan (*Mallotus villosus*) est considéré comme une des principales espèces de poissons du nord-ouest de l'Atlantique en raison de son importance commerciale et de sa qualité de fourrage. L'auteur reprend certains aspects de la biologie du capelan et traite aussi de la distribution, du frai, des schèmes migratoires, de la différenciation des stocks, de la biologie des populations et de la position du capelan dans la chaîne trophique du nord-ouest de l'Atlantique. La pêche hauturière commerciale du capelan, qui a débuté en 1972, a atteint un sommet en 1976 et a décliné depuis. L'auteur analyse la structure et la gestion de la pêche commerciale. La situation des populations a été déterminée grâce à un modèle de production excédentaire, à des techniques acoustiques et aussi à des modèles analytiques; les résultats obtenus avec les modèles analytiques montrent que le grand nombre de sujets dans la classe d'âge 1973 a donné lieu à une abondance relative de capelan au milieu des années 1970. Les quantités ont été relativement faibles dans les classes d'âges 1974 à 1978 et la biomasse du capelan a diminué vers la fin des années 1970. Les taux de mortalité causée par la pêche, calculés à l'aide des modèles analytiques, ont été faibles dans les stocks des divisions de la Northwest Atlantic Fisheries Organization 2J3K et 3L, ce qui indique que la pêche n'a pas concouru de façon appréciable à la baisse des populations. Une forte pression de la pêche sur le stock de la division 3N0 pourrait en avoir accentué le déclin. L'auteur revoit les facteurs qui influent sur la dynamique des populations de capelans et les effets possibles des fluctuations de l'effectif des populations sur les prédateurs de cette espèce. Il expose également le programme de recherche sur le capelan.

3, Introduction

It is probable that capelin (*Mallotus villosus*) is one of the most important fish species in the northwest Atlantic because of its commercial importance (1980 landed value $3.5 million) and its position as a forage species (Bailey *et al.* 1977, Winters and Carscadden 1978). The importance of capelin as a food species for other marine animals has long been recognized (Templeman 1948), but recently capelin has generated a great deal of interest both from the general public and the scientific community. This interest has arisen largely as a result of a commercial capelin fishery that developed in the early 1970s and the potential impact of this fishery on the capelin stocks themselves and on predator stocks, many of which are commercially important.

It is the purpose of this paper to review some aspects of capelin life history, the history of the commercial fishery and its management, the population dynamics of capelin, the possible impact of fluctuations of capelin on its predators, and the research program on capelin in the Newfoundland area.

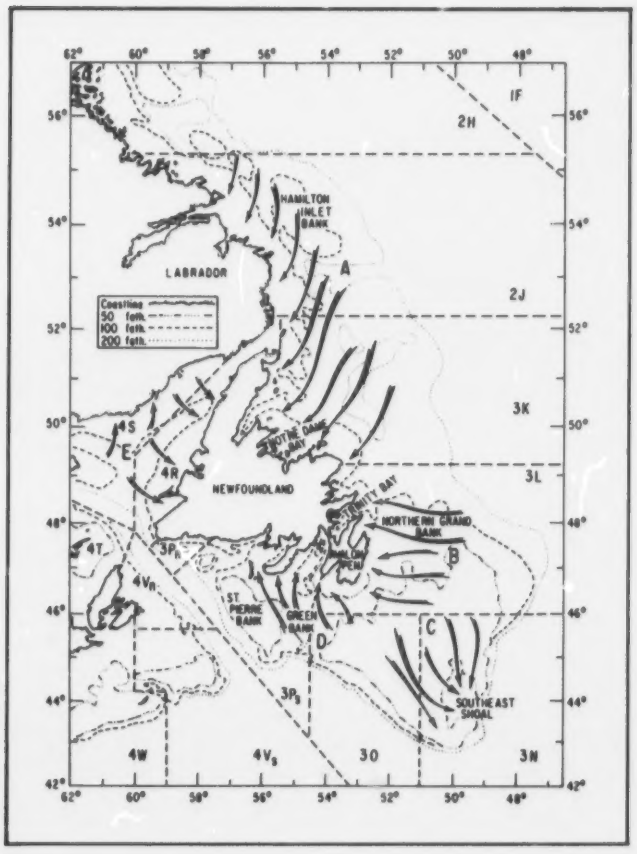
4. Life history

Capelin (or caplin) are small, silvery fish closely related to smelt. They are a cold-water, pelagic, schooling species inhabiting arctic and subarctic seas in the Atlantic and Pacific oceans. In the eastern Atlantic, capelin occur from western Norway to northern Russia and are widely distributed throughout the Barents Sea. They are also abundant around Iceland and Greenland. On the east coast of North America, capelin occur from Hudson Bay to Nova Scotia, but are most abundant around Newfoundland and Labrador. In the Pacific, capelin occur from Alaska to Juan de Fuca Strait and from the Sea of Chukotsk to Japan and Korea (Jangaard 1974).

The relative distribution of capelin in the coastal zone varies seasonally but undoubtedly peaks in June and

July, when beach spawning occurs. At other times of the year, capelin can be found in large concentrations in the offshore waters. Although the distribution of young capelin is not well defined, the distribution and migration patterns of adults are better known and spawning stocks of capelin have been identified. There are five major stocks in the Newfoundland area: Labrador–Northeast Newfoundland stock, NAFO[1] div. 2J3K, (A); Northern Grand Banks – Avalon stock, NAFO div. 3L, (B); South Grand Banks (Southeast Shoal) stock, NAFO div. 3N0, (C); St. Pierre – Green Bank stock, NAFO div. 3Ps, (D); Gulf of St. Lawrence stock (E) (Fig. 1). Some of these major stocks (e.g. Labrador – Northeast Newfoundland and Gulf of St. Lawrence) may be composed of a number of substocks (Winters 1974*a*, Sharp *et al.* 1978). These stocks have been identified through the knowledge of seasonal distribution patterns and growth differences (Campbell and Winters 1973, Winters 1974*b*), meristic (Sharp *et al.* 1978, Carscadden and Misra 1980) and morphometric (Sharp *et al.* 1978) characters, and the fishing patterns of the commercial capelin fleet. Like most species of fish, there is some degree of stock overlap during some part of the life cycle. Because most of the commercial fishery occurred on only three of the stocks (div. 2J3K, div. 3L, and div. 3N0 stocks), subsequent discussion will be restricted to capelin occurring in these areas.

Figure 1
Map showing major stocks and migration routes of mature capelin. Alpha-numeric designations (e.g. 2H, 2J, 3K, etc.) are NAFO divisions. A. Labrador – Northwest Newfoundland (NAFO div. 2J3K) stock. B. Northern Grand Banks – Avalon (NAFO div. 3L) stock. C. South Grand Banks (Southeast Shoal – div. 3N0) stock. D. St. Pierre – Green Bank (NAFO div. 3Ps) stock. E. Gulf of St. Lawrence stock. (Modified from Campbell and Winters 1973)



The Notre Dame Bay area is known to be an overwintering area for part of the Labrador – Northeast Newfoundland stock. It seems probable that capelin also overwinter in parts of NAFO subarea 2; capelin have been taken in research catches late in the year in this area and there is no known northward migration in the spring from div. 3K to the inshore spawning grounds in subarea 2. During June and July, mature capelin move inshore to spawn on beaches in northeastern Newfoundland and Labrador. After spawning, most fish die. The few spawning survivors move offshore in late summer and join immature fish to form feeding schools. Feeding is heavy from August to November and large schools are found in offshore waters from Labrador to northeast Newfoundland.

The northern Grand Bank – Avalon and Southeast Shoal stocks appear to mix and overwinter on the northern part of the Grand Banks (Campbell and Winters 1973, Carscadden and Misra 1980). During late winter and early spring the fish become active, form feeding schools, and begin a migration to the spawning grounds. The northern Grand Banks – Avalon stock moves inshore to spawn on Newfoundland beaches while the Southeast Shoal stock moves south over the Grand Banks to spawn on sandy substrate on the Southeast Shoal. Spawning in both areas occurs during June and July and post-spawning mortality is high at this time. Spawning survivors are believed to move to the northern Grand Banks area for feeding and overwintering.

There are differences in the timing of spawning in different areas. Spawning on the west and south coasts of Newfoundland usually begins in late May. Spawning time usually becomes later further to the north such that spawning in Labrador may not occur until August in some years (Templeman 1948). Spawning on the Southeast Shoal, the only known offshore spawning area for capelin, occurs in June and July.

The general environmental conditions necessary for spawning have been characterized. Capelin spawning inshore in Newfoundland and Labrador prefer water temperatures of 5.5–8.5°C and pebbles ranging in size from 0.5 to 2.5 cm in diameter (Templeman 1948). Spawning normally occurs at night or on dull cloudy days, although there are exceptions. On the Southeast Shoal, spawning occurs in a water depth of approximately 50 m where bottom temperatures are 2–4°C (Pitt 1958*a*).

Inshore spawning normally occurs for 4–6 weeks; most spawning occurs on the beaches, but if water temperatures on the beach become too high the fish will spawn in deeper water adjacent to the beaches. Deepwater spawning appears to be more common on the west coast of Newfoundland, apparently because the water temperatures near the beaches are too high by the time the capelin are ready to spawn (Templeman 1948). The extent of deepwater (non-beach) spawning is probably very variable from year to year and other factors besides water temperature on the beach may exert an influence.

Capelin mature at 3 or 4 years of age with faster growing fish maturing earlier (Winters 1974*b*). In the

[1]Northwest Atlantic Fisheries Organization (formerly ICNAF, the International Commission for Northwest Atlantic Fisheries).

spawning populations, 3- and 4-year-olds usually predominate (Fig. 2), although other ages, including two, five, six, and seven do occur in varying proportions. Spawning mortality is high, usually greater than 80% (Carscadden and Miller 1980*a*).

There is no doubt that capelin are important as a forage fish in the Newfoundland area. There have been many feeding studies conducted on predators that indicate that at some time of the year, capelin are an important component of their diet. Perhaps the most extensively studied capelin predator is cod (*Gadus morhua*) and there are a number of studies (see Akenhead *et al.* 1982, Lilly 1981, Lilly *et al.* 1981 for reviews) that substantiate the observation that cod consume capelin. It is possible to describe the broad seasonal patterns of cod predation on capelin in div. 2J3KL and div. 3N0 and the following description is taken directly from Lilly *et al.* (1981).

> Predation is apparently most intense on the north slope of the Grand Bank in winter and spring, in the Avalon Channel and on the northwestern Grand Bank in spring, on the northern Grand Bank and inshore all along the coast in late spring and summer, and along the coastal shelfs of 2J3K and on the Hamilton Inlet Bank in late summer and autumn. The predation pattern is highly seasonal in the region of Hamilton Inlet Bank, but much less so on the northern Grand Bank. Predation by cod on capelin in 3N0 appears to be largely confined to spring and summer.

In spite of numerous feeding studies Lilly *et al.* (1981) point out that "there is no estimate, based on adequate seasonal and spatial sampling, of the contribution of capelin to the total food consumption of a single cod stock in a given year." However, several studies have estimated that for the Newfoundland area in general, capelin comprise about 30% of the cod's diet (Akenhead *et al.* 1982).

Although cod is the capelin predator that often evokes the most concern, other marine species feed heavily on capelin as well. Capelin accounts for 45–100% of the food of adult salmon (*Salmo salar*), depending on size, in Newfoundland coastal waters (Lear 1972). Greenland halibut (*Reinhardtius hippoglossoides*) in the length range of 20–80 cm feed heavily on capelin (Lear 1969) and American plaice (*Hippoglossoides platessoides*) (20–49 cm) in div. 3L depend on capelin for 14–38% of their food (Pitt 1973). Haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Limanda ferruginea*), winter flounder (*Pseudopleuronectes americanus*), skates, sea ravens, and a variety of other demersal species consume large quantities of capelin eggs and capelin during the spawning season (Pitt 1958*b*, Templeman 1968).

Marine mammals also feed heavily on capelin. Capelin are an important food for whales, including fin whales (*Balaenoptera physalus*) (Mitchell 1975), minke whales (*B. acutorostrata*), sei whales (*B. borealis*) (Sergeant 1963), and humpback whales (*Megaptera novaeangliae*) (Lien 1980), in the Newfoundland area. Sergeant (1973) has estimated that at least 25% of the diet of harp seals (*Pagophilus groenlandicus*) is capelin and other less abundant species of seals such as hooded (*Cystophora cristata*), grey (*Halichoerus grypus*), and harbour (*Phoca vitulina*) seals, also consume significant quantities of capelin.

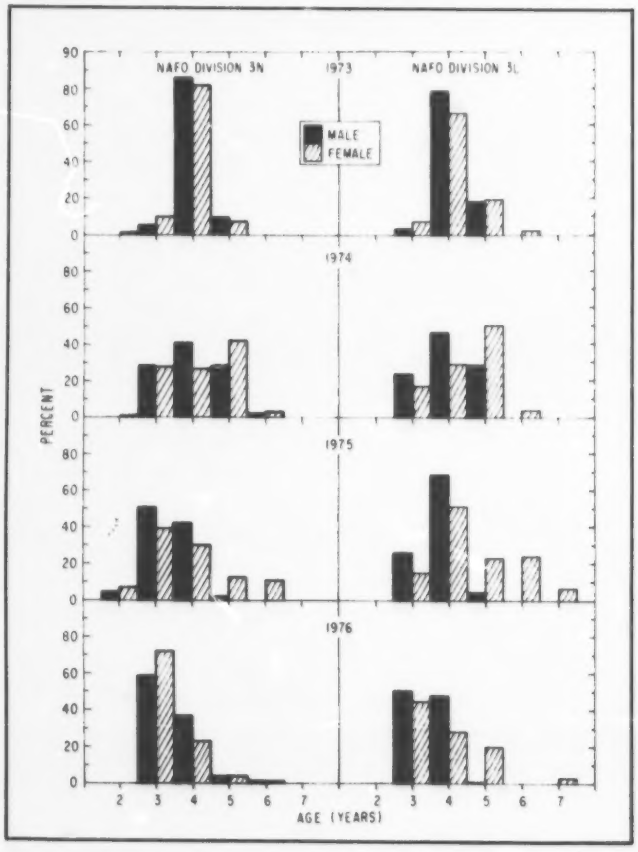
Seabirds are also capelin predators; murres (*Uria* spp.) (Tuck 1961), Atlantic Puffins (*Fratercula arctica*) (Nettleship 1972), Greater Shearwaters (*Puffinus gravis*) (Brown *et al.* 1981), Northern Gannets (*Morus bassanus*) (Montevecchi and Porter 1980), Black-legged Kittiwakes (*Rissa tridactyla*) (Maunder 1971, Winters and Carscadden 1978), and the *Larus* gulls (Pierotti 1979) all feed on capelin (see Brown and Nettleship, this volume, for details).

4. The fishery and its management

It is only in the last decade that people have become significant predators of capelin although capelin have been taken during the spawning season for decades. It has been estimated that prior to the 1950s, 20 000–25 000 t of capelin were taken annually in Newfoundland for bait and fertilizer and to a lesser extent for food for dog teams (Templeman 1968, Barnes 1974). However, with the decline in the use of dog teams and in gardens and less demand for capelin as bait, inshore landings declined considerably. During the 1970s, interest in capelin as a commercial species increased with effort being concentrated in the offshore area in the early and mid 1970s and in the inshore area in the late 1970s.

In 1972, the first substantial offshore catches of about 70 000 t of capelin were reported. These catches increased rapidly, peaking in 1976 at about 370 000 t and declining since then. The catches were taken at different

Figure 2
Example of age-compositions of mature capelin populations from div. 3L and div. 3N, 1973–76



times of the year in different areas and details of the catches by areas (div. 3L, div. 3N0, and div. 2J3K) are given in Figures 3, 4, and 5.

The annual offshore capelin fishery normally began in March or April on fish, most of which were maturing and feeding, on the northern Grand Banks (div. 3L). Thus, fish from two stocks, the northern Grand Bank–Avalon stock and the Southeast Shoal stock, were fished at this time. Most of the vessels in this fishery were USSR midwater trawlers. The fishing fleet followed the capelin as they moved to their spawning grounds; however, once the inshore spawning component entered Canadian territorial waters, the fleet followed the Southeast Shoal (div. 3N0) capelin to their spawning grounds where the fishery on spawning capelin continued into July. Most of the vessels operating on the Southeast Shoal were USSR mid-water trawlers and Norwegian purse seiners.

The fishery in div. 3L developed very rapidly with the peak catch reported in 1974, followed by a gradual decline from 1975–80 (Fig. 3). In 1975, Canadian ports were closed to the USSR fishing fleet because Canadian authorities accused the Soviets of taking approximately double their quota in div. 3L. If true, the catch in 1975 in Figure 3 should be approximately 60 000 t. In addition, the "inshore" catch in 1974 is shown at approximately 8000 t, higher than the preceding and following years. This may be an anomaly caused by the grouping of the data; in the present grouping, Canadian catches were assumed to have been taken inshore. However in 1974, some catches were reported from large (500–999 GRT) purse seiners chartered by Canadian companies. Thus, the catches may have been taken offshore and the inshore catch estimates for 1974 may be overestimated and the offshore catch estimates underestimated. In general, the trend of catches for div. 3L since 1974 has been a decrease in the offshore portion and in increase in the inshore portion. Some unknown fraction of the div. 3L offshore catch may have been fish from the Southeast Shoal stock.

The catches (Fig. 4) of the Southeast Shoal stock (div. 3N0) rose rapidly from about 21 000 t in 1972 to a level of about 100 000 – 132 000 t for 4 years between 1973 and 1976 and dropped quickly to 47 000 t in 1977 and 5000 t in 1978. The fishery was closed in 1979 and has remained closed since then. It was the conclusion of scientists that "the intense commercial fishery on the spawning grounds in div. 3N may have substantially reduced the spawning stock size in recent years, and the possibility of recruitment overfishing should be taken into account" (Anon. 1979).

Each year when the fishery on the Southeast Shoal stopped with the cessation of capelin spawning, the attention of the fleet shifted to div. 2J and div. 3K in late August or early September. This fishery, which caught feeding capelin most of which would mature and spawn the following year, was prosecuted mainly by USSR midwater trawlers and continued until November or December.

The first large catch in the div. 2J3K capelin fishery was reported in 1972 at 46 000 t. Catches peaked in 1976 at about 216 000 t and declined after than to about 5000 t in

Figure 3
Nominal catches (metric tons) of capelin in NAFO div. 3L, 1970–80

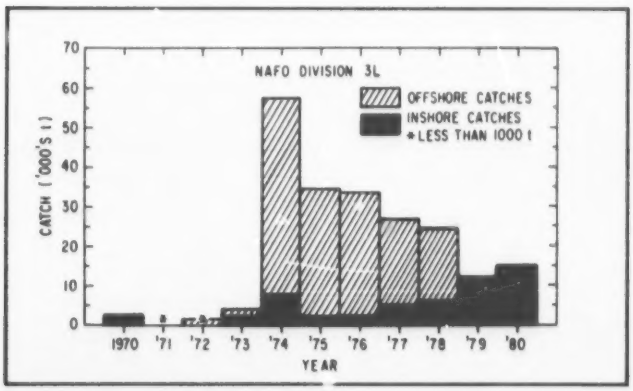


Figure 4
Nominal catches (metric tons) in NAFO div. 3N0, 1970–80

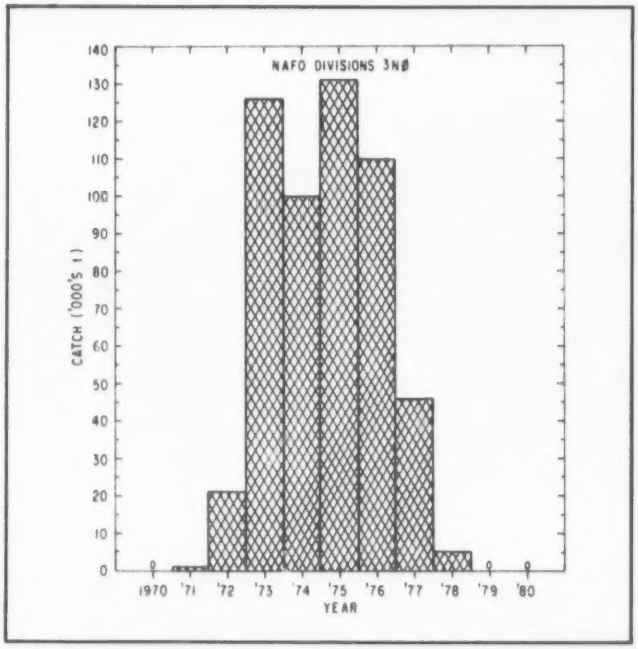
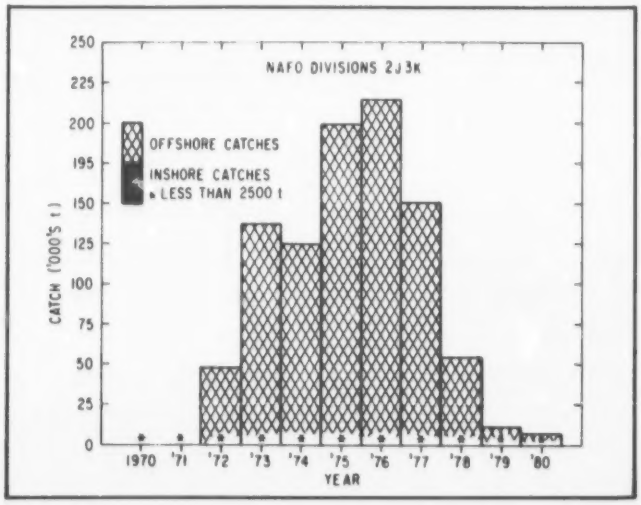


Figure 5
Nominal catches (metric tons) of capelin in NAFO div. 2J3K, 1970–80



1980. During 1970–80, inshore catches remained at a low level below 2500 t (Fig. 5).

The management of capelin came under jurisdiction of ICNAF, and later NAFO, until Canada extended its fisheries jurisdiction to 200 miles (1 Jan. 1977). At this time, the div. 2J3K stock came solely under Canadian management because it occurred completely within Canadian jurisdiction although Canada has continued to request that biological advice be provided through NAFO. The div. 3L and div. 3N0 stocks overlap the Canadian zone and biological advice and management recommendations have continued under the auspices of NAFO. The biological advice provided for the management of capelin has, with few exceptions, beeen adopted by the fisheries managers in NAFO and in Canada and as a result, the biological advice and some of the rationale for that advice is provided below.

The biological advice, provided through ICNAF and later NAFO, was initially requested because of the increasing commercial offshore fishery during the early 1970s. The first advice concerning the total allowable catch (TAC) of capelin pertained to 1974 when it was recommended by the Standing Committee on Research and Statistics (STACRES) of ICNAF that the catch should not exceed 250 000 t. The following year (1975) it was recommended that the TAC could be increased to 500 000 t and maintained for 3 years. Furthermore, it was noted that the fishery should be restricted to mature capelin approaching and during the spawning season, and countries participating in the fishery should conduct surveys of both the adult and juvenile stock to monitor the effect of the fishery. Also in 1975, a crude estimate of relative stock size resulted in a recommendation that 300 000 t could be allocated to the northern area (div. 2J3K) and 200 000 t to the southern area (div. 3LN0Ps). A further subdivision of the southern TAC, based on various biological factors, was also recommended at that time:

> Consideration was given to the question of further subdivision of the TAC on the basis of existing knowledge of stock differentiation. It was concluded that further subdivision of the northern TAC was not practical at the moment due to insufficient knowledge of stock separation in this area. In the south, however, there is evidence to suggest that the fishery in Div. 3L may operate on several separate spawning components which spawn later inshore in Div. 3L, on the Southeast Shoal, and possibly in Subdiv. 3Ps. In 1974, Div. 3L supported a large fishery, while the catch in Subdiv. 3Ps was small. To preclude rapid development of a fishery on a possibly small stock in Subdiv. 3Ps, STACRES advises that an amount of 10 000 tons from the southern TAC be reserved as a maximum permissible catch from Subdiv. 3Ps, with the proviso that any part of this amount could be taken in Div. 3N0 if not taken in the former area. For the southern area as a whole, it was concluded that it would be desirable for the fishery to be concentrated as much as possible on the concentrations of mature capelin in Div. 3N0 to minimize potential adverse effects on capelin and other species. If this were practical, it would avoid the possibility of overfishing any one of the spawning components present in Div. 3L earlier in the season, and, for the inshore spawning stock, it would avoid the possibility of adversely affecting inshore migration and feeding success of the Div. 3L cod. If the principle of directing the southern fishery toward the spawning concentrations is accepted by the Commission, this objective could be achieved by further subdivision of the southern TAC. For example, it could be achieved by setting an upper limit for the Div. 3L fishery of 50 000 tons, with the proviso that any part of this amount not taken in Div. 3L could be taken in Div. 3N0.
>
> To summarize, the management regime in the southern area would then consist of an overall maximum TAC of 200 000 tons, no more than 10 000 tons of which could be taken in Subdiv. 3Ps and no more than 50 000 tons of which could be taken in Div. 3L. If these maxima were not achieved in Subdiv. 3Ps and Div. 3L, the uncaught amounts could be added to the catches in Div. 3N0. (Anon. 1975)

The biological advice remained essentially unchanged until 1979 when evidence of poor recruitment in the capelin population resulted in a recommendation of reductions in the TACs. STACRES advised that the 1979 TAC in div. 3LN0 should be 16 000 t and to protect the spawning stock in div. 3N and during its migration through div. 3N0, there should be no commercial fishery for capelin in div. 3N0. This meant that 16 000 t could be taken only in div. 3L. It was agreed by the NAFO commissioners that there would be no offshore fishery for capelin in div. 3L and Canada claimed only 10 000 t to be taken inshore. Therefore the TAC for capelin in div. 3L in 1979 was essentially 10 000 t. In the northern stock, it was recommended that the 1979 TAC be reduced from 300 000 to 75 000 t. The recruitment prognosis remained poor in 1980 and the biological advice remained unchanged for the stocks in div. 3LN0 that is, a TAC of 16 000 t with no fishing in div. 3N0. In the north, the advice was to close the fishery or allow a small nominal TAC. It was noted that a small fishery of 10 000–15 000 t in the north would allow scientists to better assess the status of the stock in 1980 and to quantify the advice for the next year. An experimental fishery with a TAC of 5000 t was conducted in fall 1980 to provide data for assessment purposes. In 1981 there was some evidence of improvement in the southern area and based on the exploitation rate that had been recommended in 1980 and 1981, a TAC of 30 000 t to be taken in div. 3L was recommended while the div. 3N0 fishery should remain closed. In the northern area, there was conflicting evidence in the scientific data and as a result, the advice remained unchanged from the 1980 advice; that is, that the fishery remain closed or a small nominal fishery of 10 000–15 000 t be allowed. An experimental fishery with a TAC of 10 000 t operated in div. 2J3K during fall 1981.

In general terms, because of the uncertainties involved in the scientific data, the known poor recruitment to the capelin stocks in recent years, and the importance of capelin as a food for other marine species, a conservative exploitation rate of 10% has been recommended since 1979. By comparison, the annual catch (ranging between 1 149 000 and 2 940 000 t) from the Barents Sea capelin stock exceeded 20% of the estimated stock size between 1974 and 1980 (Anon. 1982).

The assessment techniques that formed the basis for the biological advice detailed above have undergone considerable evolution, expansion, and improvements since the mid 1970s, but in general, the international capelin fishery developed faster than the scientific base. There had been some studies on the biology of capelin (e.g. Templeman 1948; Pitt 1958*a*, 1958*b*; Winters 1966, 1970*a*, 1970*b*) but detailed information on population dynamics of capelin, especially biomass estimates, was not available during the early 1970s. Since 1974, there have been three general methods of assessing the capelin stocks; a surplus production model, acoustic estimation, and analytical models.

The use of the three assessment methods has shown a trend over time. During the early phase of the fishery, acoustic estimates and the surplus-production model were the only sources of information. Both types of estimates were recognized as being crude but they were accepted as indications of the magnitude of the capelin resource. The surplus-production model was used only in the early years of capelin assessments whereas the acoustic method has been used since 1974. Eventually the acoustic estimates were used only as indications of relative abundance. As the fishery continued through the 1970s, there were enough data accumulated to develop the sequential-capelin-abundance models. In the most recent years, these models have been used as the most reliable indications of stock status and as a starting point for projections. Ironically, these models have depended on the fishery as a data source and the results from the models have been largely responsible for the advice to reduce the total allowable catch.

The surplus-production model was first developed in 1973 (Campbell and Winters 1973) and expanded in 1975 (Winters 1975, later revised by Winters and Carscadden 1978). Although it is extremely crude, the model was used to provide biological advice and was intended to provide a first estimate of potential long-term annual yield of capelin. It was recognized that many species of marine fish, mammals, and seabirds fed extensively on capelin. Since it was known that the stocks of many of these predators had declined during the 1950s and 1960s, it was assumed that there would be capelin available to a commercial fishery in the 1970s that previously would have been necessary to sustain the predator stocks. Three predators, cod, whales, and seals, were chosen for this analysis because there were estimates of both abundance and of capelin consumption (albeit crude in some cases) available for these animals. It was estimated that annual capelin consumption by cod between the mid 1950s and mid 1960s, when adjusted for density-dependent changes in cod growth, declined from 3.97 million metric tons to 3.0 million metric tons, releasing 0.97 million metric tons of capelin. Estimates of feeding by harp seals suggested that consumption of capelin had declined from 432 000 to 300 000 t due to the attrition in the seal population. Therefore the surplus production of capelin released by the decline in the harp-seal population was 132 000 t. For fin whales, the annual consumption of capelin was estimated to have declined from 360 000 to 250 000 t releasing 110 000 t of surplus production of capelin. The surplus production of capelin released by the decline in the population of minke whales was estimated to be 15 000 t. The total excess production of capelin released by the decline in the abundance of its major predators (cod, seals, and whales) and available for utilization by people was estimated to be about 1.25 million metric tons.

It was noted (Winters 1975, Winters and Carscadden 1978) that these calculations were extremely crude and relied on a number of untested assumptions. Furthermore, this estimate was an average, and considerable variation in stock size and potential catch could be expected due to the large recruitment variations known to occur in capelin (Gjosaeter 1972). The authors (Winters 1975, Winters and Carscadden 1978) suggested that the TAC should not exceed the lower limit of fluctuation in spawning stock size. In this case, the TAC should not exceed 20% of the 1.25 million metric tons of surplus capelin or 250 000 t. In a later study of cod feeding, Minet and Perodou (1978) estimated that cod in div. 2J3KL3Pn4RS consumed 2.24 to 3.8 million metric tons of capelin annually in the years 1965–69, a figure that was in reasonable agreement with that of Winters (1975) and Winters and Carscadden (1978).

Acoustic estimates have been produced primarily by Soviet and Canadian scientists although one early estimate (Dragesund and Monstad 1973) was produced from an exploratory survey by the Norwegians. All of the acoustic estimates have been derived using vertical echo sounders and integration of the voltage of the returned signal (echo integration) — a technique commonly used to estimate abundance of schooling fishes such as capelin in the Barents Sea (Dommasnes 1977) and blue whiting (Anon. 1981) in European waters. In the northwest Atlantic, the Soviets have the longest time series of acoustic estimates of capelin, beginning in 1974 in the northern area (div. 2J3K) and 1975 in the southern area (div. 3LN0). The Canadian estimates are more recent, with the first estimate in the northern area coming from a 1977 survey and in the southern area from a 1979 survey.

Biomass estimates derived from the Soviet and Canadian acoustic surveys are shown in Tables 1 and 2 respectively. It is not possible to discuss the details of each survey here but it should be noted that there are factors, both physical and biological, that affect the results of these

Table 1
Biomass estimates of capelin (metric tons) from Soviet surveys in div. 2J3K and div. 3LN0, 1974–80 (from Bakanev 1981)

Year/stock	2J3K	3LN0
1974	1 334 000	—
1975	981 800	1 050 000
1976	748 900	680 000
1977	505 700	1 000 000*
1978	59 000	230 000
1979	14 500	483 000
1980	20 200	+†

*Up to 1977, mainly surveyed mature stock in div. 3N0; after 1977, mainly surveyed in div. 3L where mixtures of mature and immature capelin and sandlance occur.
†Few mature capelin, immature capelin mixed with sandlance — no biomass estimate possible.

Table 2
Standardized acoustic biomass estimates (metric tons) for capelin from Canadian acoustic surveys (from Miller and Carscadden 1981)

Year/stock	2J3K	3L	3N0	3LN0
1977	41 500	—	—	—
1978	14 000	—	—	—
1979	10 400	37 400	4 600	42 000
1980	—	16 700	9 900	26 600
	—	(2 600)*	(1 300)*	(3 900)*

*Adult portion in 1980. Most adults in div. 3L have already migrated to spawning grounds at time of the survey.

surveys and such factors are usually discussed in each survey report (all in ICNAF/NAFO research document series). Hence, the original reports should be consulted for the authors' assessments of the reliability of the estimate and how such factors affected the final estimate. In spite of this note of caution, it is obvious that the results from the Soviet surveys (Table 1) indicate a decline in capelin stocks, especially in the northern stocks. Although the Canadian time-series (Table 2) is shorter, the results from these surveys also show a decline in capelin stocks in recent years.

The results of the Soviet and Canadian surveys are not directly comparable. The results are often conducted at different times of the year and usually cover somewhat different areas. The equipment used by the two countries and calibration techniques differ markedly. For instance, the Canadian method involves a calibration of the acoustic system using a calibrated hydrophone. In some of the Soviet surveys (e.g. Ermolchev *et al.* 1979, 1980) the echo integration of capelin was calibrated by echo counting while in others (e.g. Bakanev *et al.* 1976, Klochkov *et al.* 1977) the calibration consisted of comparison of the echo signal to density estimates calculated from photographs of capelin obtained by lowering a camera into capelin schools. These differences may have contributed to differences in the estimates; however, it is not clear why the Canadian estimates are so much lower than the USSR estimates. Although not comparable between countries, the biomass estimates have generally been accepted as internally comparable.

It should be emphasized that although the Canadian acoustic estimates are given in metric tons, they are used only as relative estimates, not as absolute values and as such, they are regarded only as trend indicators. Furthermore, in recent years, the Soviet acoustic estimates have been used mainly to indicate trends in abundance rather than as absolute estimates of abundance.

The decision to use the Canadian acoustic estimates as relative estimates arose for two reasons. First, there were relatively few measurements of target strength available for capelin: the target-strength values are critical for biomass estimation, and errors in target strength can create serious errors in the final biomass estimate. There was no information available on swimming angle of capelin in the field and it is known that target strength can change radically with swimming angle of the fish (Nakken and Olsen 1977). Second, there was a reluctance on the part of other scientists to accept estimates derived from acoustics, a relatively new technology to most, as valid indications of stock status. Thus, the conservative approach of using the acoustic estimates as relative was adopted.

Like all survey techniques, hydroacoustics has both advantages and disadvantages, and these are summarized in Table 3 in comparison to other techniques. Because of the biology of capelin, hydroacoustic surveys, augmented by mid-water and bottom trawling to provide information on biology and species composition, appears to be the most effective way to provide indices of abundance from surveys for capelin.

Most of the analytical analyses employed have been developed and used since 1978 and except for two (Gulimov and Kovalev 1957, Seliverstov and Serebrov 1979) all have involved sequential population analysis. The high natural mortality in capelin, especially the mortality incurred during spawning (Winters and Campbell 1974) prevented the use of standard sequential population analyses such as virtual population (Gulland 1965) or cohort analysis (Pope 1972). As a result, new sequential-capelin-abundance models (SCAM) were developed to use pertinent biological and fisheries information and provide a historical perspective of the dynamics of capelin in the Newfoundland area (Carscadden *et al.* 1978, Carscadden and Miller 1979, Miller and Carscadden 1979, Carscadden and Miller 1980*a*, Carscadden and Miller 1981, Carscadden *et al.* 1981).

These models are similar to virtual population analysis and cohort analysis both in their design and mechanics. They attempt to calculate for any year-class its age-specific size and fishing mortality rate based on such input parameters as catch-at-age and natural mortality rate. Like cohort

Table 3
Advantages and disadvantages of various survey methods used in fisheries research (from Ulltang 1977)

Method	Applicability	Discrimination between species	Result obtained		Time/ spatial coverage	Craft and equipment	Operation cost	Time for data processing
			Variance	Potential bias				
Fishing survey	Demersal and to some extent pelagic fish	Excellent	Large	Small	Limited	Vessel and fishing gear	High	More or less long
Acoustic survey	Pelagic and to some extent demersal fish	Poor	Small	More or less large	Good	Vessel and acoustic instrument	Low*	Short
Sighting survey	Pelagic fish	Poor	Large	Large	Good	Aircraft or vessel	Variable	Short
Eggs and larval survey	Demersal and pelagic fish	Excellent†	Large	Large	Limited	Vessel and collector	High	Long, laboratory work
Tagging	Demersal and pelagic fish	Excellent	Highly variable‡	Highly variable, often large		Vessel and fishing gear for releasing, fishery and eventual equipment for recovery	Variable	More or less long

*Cost of acoustic instruments is rather high and not included in the operation cost.
†Except in cases where the eggs or larvae of different species cannot be reliably identified. This is a bigger problem for eggs, particularly in early development stages, than for larvae.
‡Is directly related to number of recaptures.

analysis, some method of estimating fishing mortality in the most recent year is necessary and in all cases to date, commercial catch rates have been used to calibrate the models and so provide an estimate of terminal fishing mortality. The models differ from cohort and virtual population analysis in that some temporal partitioning occurs and the different mortality rates (i.e. high spawning mortality rate at one time of the year and natural mortality rate at other times) are applied to the population estimates at the appropriate time of the year within the model. Because recruitment to the mature portion of the population is essentially equivalent to maturation rate and the fishery operates primarily on mature fish it was necessary to incorporate annual age-specific maturation rates into the models as well.

These models are quite detailed and require a large body of data from the fishery and sometimes from research cruises. Catches from the commercial fishery are broken down into age-classes using length, weight, and age data collected from the fishery. Estimates of spawning mortality (Carscadden and Miller 1980*a*) and maturation rate (Winters *et al.* 1980) have been calculated and are necessary for the models. The models have to be calibrated in some way; we have used catch-per-unit-effort data but other indices of abundance, such as estimates from a hydroacoustic survey could also be used. In the SCAM 2J3K, estimates of selection by the fishery are necessary and these have been derived from comparisons of age-composition of the capelin taken by the commercial fishery and by research vessels.

The models have undergone various modifications in their development and use. For instance the SCAM for the div. 2J3K capelin stock (SCAM 2J3K) has changed little since its development in 1979 (Miller and Carscadden 1979; Carscadden and Miller 1980*a*, 1981). On the other hand, SCAMs for the southern area have changed dramatically such that the earliest version (Carscadden *et al.* 1978) and a later version (Carscadden and Miller 1979) have not been used recently. These earlier versions have been dropped because of the cessation of commercial fisheries in the areas of interest. In the most recent assessment of the capelin stocks (February 1981) two versions of the models — SCAM 2J3K (Carscadden and Miller 1981) and SCAM 3L (Carscadden *et al.* 1981) were used. The results of these models, showing trends in biomass and historical catches, are given in Figures 6 and 7. It is obvious that the catches have been low in relation to the biomass estimates resulting from these models.

Unfortunately these models do have some drawbacks. Sequential population models (cohort, virtual population analysis) are useful because, due to the nature of the mathematics, the further back in time the calculations are carried, the less sensitive are the population estimates to the input fishing mortality. In addition, these models are potentially more useful with species that have a number of age-classes in the population and natural mortality rates that are equal to or lower than the fishing mortality rates. Since capelin have relatively few age-classes, high natural mortality rates, and a relatively short history of fishing on a large scale, the sequential-capelin-abundance models converge less quickly than models using multi-age species with a longer fishery. The models have also been found to be very sensitive to the input parameters of age-specific maturity and age-specific spawning mortality. Like all sequential population models they are fishery-oriented, that is, much of the basic data is derived from the fishery itself. In a

Figure 6
Exploitable capelin biomass (metric tons), estimated using sequential-capelin-abundance models, and catches in div. 2J3K, 1972–80

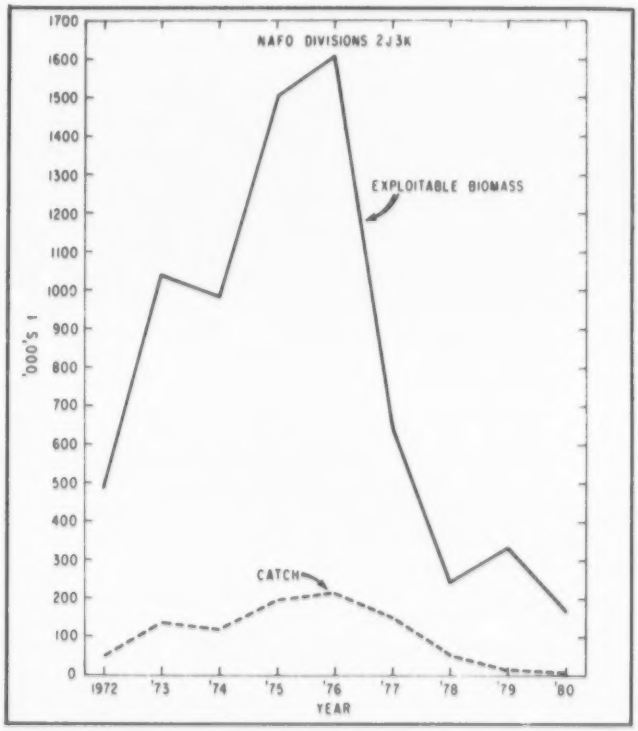
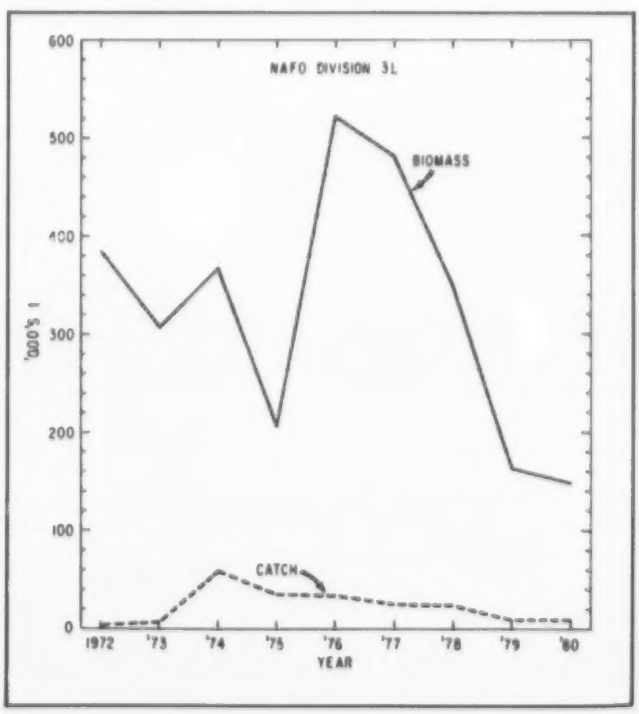


Figure 7
Total (ages 3, 4 and 5) capelin biomass (metric tons) 1 Jan. each year, estimated using sequential-capelin-abundance models and catches in NAFO div. 3L, 1972–78



dynamic fishery, which the capelin fishery has been, this has resulted in some limitations in their use, especially in recent years. The fact that the capelin fishery in its early years was a foreign fishery operating in international waters caused some difficulties in data collection as well and, in some cases, we have been forced to use data with little or no knowledge of the scientific basis of its collection.

In spite of these disadvantages, the models do have several advantages. They make use of a vast body of fisheries-related data that might otherwise not be used. They have provided a historical perspective of capelin population dynamics — in some cases, in years when no other estimates were available.

5. Population dynamics and the impact on predators

The sequential-capelin-abundance models have provided the most valuable insights into the population dynamics of capelin. For instance, year-class strength in div. 2J3K, measured as 2-year-olds, has varied such that the strongest year-class (1973) was over 30 times the strength of the weakest year-class (1975 and 1976); yet because of a number of age-classes (five in the div. 2J3K analysis), the largest calculated biomass (1975) was only seven times the smallest biomass (1980) (Table 4). The trends in biomass in two stocks, the div. 2J3K stock and the div. 3L stock, indicate that because of the presence of the strong 1973 year-class in the total capelin population the biomass peaked in the mid 1970s. However, five consecutive year-classes (1974–78) have been relatively weak resulting in low capelin biomasses.

The pattern of large variations in abundance of year-classes is typical of pelagic fish species. For instance, MacCall (this volume) reported that anchovy abundance off southern California varied over 30-fold in 30 years and that the Peruvian anchoveta and the sardines in Peru and California were also variable in abundance. Herring also exhibit variable year-class strengths. In the southern Gulf of St. Lawrence herring stock, two exceptionally strong year-classes (1958 and 1959) appeared after a fungus (*Ichthyosporidium hoferi*) had caused large mortalities (Winters 1976). Other relatively good year-classes in this stock in recent years were the 1967, 1968, and 1974 year-classes while all other year-classes have been lower in abundance. In the recent series of year-classes (1967–78), the weakest and strongest vary by a factor of seven (Cleary 1981).

In many pelagic stocks, the natural fluctuations in abundance are often complicated by the presence of fishing mortality and in some cases (e.g. Norwegian spring-spawning herring [Dragesund *et al.* 1980]) fishing mortality may be affecting recruitment. Based on the analyses using the sequential-capelin-abundance models, fishing has not been the cause of the decline for the div. 2J3K (Carscadden and Miller 1981) and div. 3L (Carscadden *et al.* 1981) stocks. Fishing mortality rates calculated from these analyses have generally been below 0.1. As has already been noted, it was the opinion of ICNAF scientists that the stock spawning on the Southeast Shoal may well have been fished too heavily.

It would appear that the capelin biomass fluctuations detected in recent years have been due to natural variation in year-class strength although the causes of this variation are not understood. Frank and Leggett (1981*a*, 1981*b*) have been studying factors affecting egg and larval mortality on a capelin spawning beach in Newfoundland since 1978. The time between egg deposition on the beach and hatching in the gravel was influenced by average incubation temperature; this incubation temperature varied between years and between cohorts in a single year and between low, mid, and high-tide locations on the beach. Water temperature, maximum and minimum air temperatures, and hours of sunlight all determined the average incubation temperatures. The interacting effects of egg density, water temperatures, maximum and minimum air temperature, hours of sunlight, rainfall, and tidal amplitude explained over 70% of the temporal and spatial variance in egg mortality. The climatic and hydrographic variables that influence egg mortality vary only slightly over most of the major spawning sites in eastern Newfoundland and southern Labrador areas, and the authors suggest that synchronous changes in these variables may contribute to the year-to-year fluctuations in capelin year-class strength (Frank and Leggett 1981*b*).

Frank and Leggett (1981*a*) have also reported that the emergence of larval capelin from beach gravel was correlated with onshore wind-induced wave action. There was a positive correlation between density of larvae in the beach gravel and length of time separating the occurrence of onshore winds. As residence time in the gravel increased, the physical condition of the larvae deteriorated. The authors suggest that year-to-year difference in wind patterns could contribute to the large annual variation in year-class strength in capelin. However, it is obvious that wind events were not the only factors affecting survival of capelin because two strong year-classes (the 1969 and 1973 year-classes) have been strong in all areas of the northwest Atlantic, including the spawning areas in deeper water on the west coast of Newfoundland (1973 year-class only because of lack of data for 1969) and the Southeast Shoal, where the effects of winds on the spawning substrate would be expected to be minimal (Frank and Leggett 1981*a*).

Table 4
Total numbers of capelin at age (billions of fish) and total biomass (metric tons) on 1 January estimated for div. 2J3K capelin stock using SCAM (Carscadden and Miller 1981). Total population at start of year ($\times 10^{-3}$) is given

	Year								
Age/years	**1972**	**1973**	**1974**	**1975**	**1976**	**1977**	**1978**	**1979**	**1980**
2	52 194 912	53 032 533	42 059 585	224 422 999	22 247 628	7 700 815	6 425 579	18 012 101	62 534 457
3	60 542 688	38 449 570	38 045 602	30 193 482	160 977 185	15 730 672	5 555 650	4 524 932	13 005 768
4	24 492 397	37 609 906	24 454 739	21 822 845	16 310 735	81 765 801	8 667 393	3 068 657	2 954 761
5	2 426 912	7 844 461	15 202 730	10 328 566	4 527 922	3 625 181	26 937 567	2 838 022	520 224
6	433 255	494 393	1 620 667	3 842 337	1 417 383	496 787	1 031 350	5 215 569	474 083
Total biomass	1 987 294	2 220 153	2 274 123	3 697 127	3 641 572	2 435 473	1 238 245	500 920	869 536

It is possible that predation has some influence on year-class variation in capelin and Dawe *et al.* (1981) investigated the effect of inshore predation by squid (*Illex illecebrosus*) on the abundance of capelin using correlation analysis. There was a negative correlation between abundance of squid and year-class strength (ages 0 and 1) of div. 2J3K capelin. However, the authors noted that there were a number of problems with their analysis, usually related to the unavailability of proper data to evaluate their hypothesis. For instance, there are no quantitative studies on squid feeding and although squid appear to have the potential to have a significant impact on prey species, the biomass of the prey species cannot be calculated because it is not known if squid prey on larvae, 0-group, 1-group, or older fish. The authors were forced to use estimates of year-class size at ages two, three, or four as indicators of abundance of age groups zero and one since neither estimates of abundance of the younger age groups nor estimates of natural mortality were available. The analysis may have been confounded by temporal trends since the time-series for capelin was only 8 years. Interestingly, in 1979 squid abundance was very high (Dawe *et al.* 1981) and the 1979 year-class of capelin appears to be very abundant (see following section). Thus, this correlation may disappear with the addition of the 1979 point.

Based on a feeding study of capelin in the Gulf of St. Lawrence, Vesin *et al.* (1981) advanced a different interpretation for the observation that in some years squid abundance was high when capelin abundance was low. They estimated that with the decline of capelin in the Newfoundland area in the late 1970s, substantial quantities of zooplankton would be released to other predators. This led them to speculate that this release of zooplankton may be important in regulating changes in year-class of other species, notably arctic cod (*Boreogadus saida*) and squid (*Illex illecebrosus*). Except for the estimates of surplus zooplankton, no quantitative analyses were presented to support the hypothesis.

The decline in capelin in recent years, has caused a great deal of concern regarding the effects this decline will have on predator stocks. Because of its importance to the Newfoundland fishery and economy and the anecdotal observations that cod follow capelin inshore (Akenhead *et al.* 1982) the effects of capelin fluctuations on populations of cod have been questioned. Although there have been no studies designed to accurately quantify the importance of capelin to cod, one study (Akenhead *et al.* 1982) did attempt to investigate the effects of fluctuations of capelin biomass on cod growth and on the inshore cod fishery using data already at hand. There was no statistically significant effect of capelin biomass on cod growth detected in this study. However, after making corrections for the biomass of cod, the authors did detect significant relationships between cod-trap catches and capelin biomass as well as between total inshore-gear catches and both capelin biomass and water temperature. Unfortunately, because of considerable uncertainty in the data, including the lack of proper data in some cases, the authors concluded that "the present analysis provides no useful evidence for testing the importance of capelin to cod but does suggest areas of concentration of future research." Furthermore, the authors concluded with the following statement:

> A lack of detailed data also hinders examination of the importance of capelin to the inshore cod fishery. Although cod and capelin tend to arrive in inshore waters at about the same time, suggesting that cod may actively follow the capelin toward shore, there is also anecdotal evidence that either species may arrive inshore unaccompanied by the other, and that the arrival of cod is also closely related to the warming of inshore waters. Elucidation of these relationships requires a site-specific study of the inshore migration, in which the abundance and movement of both cod and capelin can be related to changes in oceanography.

Recently, the failure of the 1977 smolt-class of salmon prompted Carter (1979, 1980) to state that the decline of capelin due to overfishing caused the failure of this smolt-class. It appeared that an unusually high mortality of this smolt-class had occurred during its first winter at sea (Reddin and Carscadden 1981). There were virtually no feeding data available to indicate whether capelin were important in the diet of salmon during their first sea-winter, but the size of young capelin in relation to smolts suggested that they would be suitable prey. Assuming that capelin were eaten by salmon, Reddin and Carscadden (1981) showed, using correlation analysis, that in some cases there were statistically significant relationships between salmon catches and abundance of young capelin. However, the authors noted that these relationships might degenerate with additional data since most of the relationships were significant only because of the 1977 smolt-class. Indeed, when the analyses were repeated (Carscadden and Reddin 1982) using data updated by one year, none of the relationships was statistically significant.

The analyses of the cod–capelin and salmon–capelin relationships failed to produce unequivocal proof of the dependence of the predator on capelin. In both analyses, the data available were not collected to test the postulated relationships, thereby making the results suspect, or in some instances, the proper data were not available. For instance, cod-trap catches were assumed to be an indicator of inshore cod abundance which further assumes that fishing effort has not changed over the time period in question. A better indicator would have been catch per unit effort which accounts for changes in effort from year to year; unfortunately, effort data were not available. In both studies, it was assumed that the predators were dependent on capelin and a change in the abundance of capelin would result in a change in the dynamics of the predator. However, the diet of both cod (Akenhead *et al.* 1982) and adult salmon (Reddin and Carscadden 1981) is spatially and temporally variable and in the absence of capelin, both species could probably feed on other prey if available. In this case, an absence of capelin probably would not result in starvation of the predator nor an immediate drop in abundance. Instead, a reliance on other prey or less prey might result in slower growth and/or reduced fecundity, if in fact there was a detrimental effect at all. Such effects would be subtle and long-term, making them more difficult to detect. During the late 1970s when capelin abundance had declined, arctic cod (*Boreogadus saida*) populations appeared to have increased in northern Newfoundland and Labrador (unpubl. data) while sandlance (*Ammodytes dubius*) (G. Winters, pers. comm.) and squid (*Illex illecebrosus*) (Dawe *et al.* 1981) increased in the Grand Banks area. All of these species would be potential prey for capelin predators.

The decline of capelin in the late 1970s has also been implicated in the increase of damage to fishing gear resulting from whale collisions (Lien 1980). Although the relationship was not established statistically, Lien (1980) suggested that a decline of the offshore capelin stock resulted in increased migration of whales to the inshore area. Sightings of humpback whales increased along the northeast coast of Newfoundland from 1974 to 1979 and sightings decreased along the south coast in 1978 and 1979 and Lien (1980) attributed this to the fact that the northern capelin stock had not declined as much as the southern capelin stocks. This postulated relationship may not be as direct as Lien suggests since in 1979 the northern stock (div. 2J3K) dropped to about one-fifth of the 1976 biomass (Fig. 6), while the southern stock had dropped to about one-third in the same period (Fig. 7). The estimates for the southern stock do not include capelin from div. 3N0 and div. 3P. However, Lien (1980) suggested that other factors have contributed to an increase in collisions of whales with fishing gear: these were an increase in the whale population, an increase in fishing effort, and an attitudinal change on the part of fisherpeople resulting in increased reporting of collisions.

Seabirds are known to feed on capelin and Brown and Nettleship (this volume) have expressed concern for seabirds, especially Atlantic Puffins, as a result of the recent decline in the capelin population. These authors note that puffins will feed heavily on capelin during the puffin breeding season when the fledging success is related to the food supply. It would seem reasonable to expect that the effects of fluctuations in capelin biomass would be more readily apparent in a predator such as puffin than a predator such as cod which apparently has a more varied diet. In fact, seabirds do exhibit wide annual variations in breeding performance and this, in combination with their life-history characteristics such as long life span, late maturity, and low reproductive rates, makes the identification of factors responsible for changes in the populations of these seabirds difficult (Nettleship 1977).

In general, although considerable concern has been expressed for the well-being of capelin predators when capelin abundance is low, it is impossible with the present data base to predict what, if any, the effects on predators would be. This is partly explained by the lack of detailed, long-term quantitative feeding data (for the fish and marine mammals, at least) which would permit a more quantitative definition of the importance of capelin to its predators. Little is known of the biology and population dynamics of potential alternate sources of prey, arctic cod and sandlance for instance, and what the effects of increased predation of these animals would be in the event of low capelin abundance. Furthermore, the natural factors affecting the abundance and behaviour of capelin predators are not understood, although there is probably a complex of environmental and biological factors operating rather than a single one such as abundance of capelin.

6. The future

It is impossible to make predictions regarding the long-term trends in capelin population dynamics. Presently, biological advice for management purposes is being provided either 1 year in advance of or early in the fishery year. The large annual variations in year-class strength and the short life cycle of the species make predictions over a longer period very uncertain. Research vessel cruises conducted by Canada (Miller and Carscadden 1981, unpubl. data) and the USSR (Bakanev 1981) have detected large concentrations of young capelin composed of the 1979 year-class in the area of the northern Grand Banks. If this year-class proves to be large (and it appears that it is) then the abundance of spawning capelin inshore in 1982 (as 3-year-olds) and possibly 1983 (as 4-year-olds) will be large. Such a phenomenon would be interesting because this large year-class would have resulted from the spawning of an adult biomass that was estimated to be one of the lowest in our time-series (see Fig. 6 and 7). Of particular interest in coming years will be the response of the Southeast Shoal population where overfishing has been implicated in its decline in comparison to spawning stocks where fishing does not seem to have been deleterious. Whether the 1979 year-class proves to be large or not, the results of the analyses to date suggest that any changes in the capelin stocks will be largely dependent on the environment rather than on the presence or absence of a conservative and controlled fishery.

The first stage in the management of capelin fishery is the provision of biological advice from the research biologists. At the present time, the capelin research revolves almost exclusively around estimation of biomass, both inshore and offshore, and attempts to estimate incoming year-class strengths. The changing pattern of the commercial fishery has made the use of the SCAMs more and more difficult, particularly regarding the calibration of the terminal fishing mortality estimates. There is a heavy commitment to offshore acoustic surveys using a newly developed microprocessor-based hydroacoustic data-acquisition system. Our research vessels will have onboard HP1000 computer systems and it is our intention to analyse much of the data collected on these acoustic cruises onboard the vessel using specially-written echo-integration programs. Our experience in the last 3 years in div. 3LN0 suggests that it will be possible not only to provide an abundance index of capelin moving inshore to spawn in div. 3L and spawning in div. 3N0, but also to estimate an abundance index for juveniles in div. 3L. The annual fall hydroacoustic survey in div. 2J3K provides an index of abundance of maturing capelin as well as information on juveniles.

There is a need for additional research on target-strength measurements of capelin, especially the factors such as depth, biological condition, and so on, that affect target strength. Through the use of underwater photographs of capelin (Carscadden and Miller 1980*b*), information on swimming angle distribution of fish is being collected and eventually these data will be used to refine acoustic estimates.

The recently developed inshore fishery is being monitored as closely as possible. Emphasis is being placed on collection of log-book data and biological data from all sectors of the fishery. Particular emphasis is being placed on Trinity Bay, an important capelin and cod area. Extra effort on the inshore capelin fishery will be expended in this bay because a detailed study on the early life history of herring and capelin will be initiated here in 1982. In addition, a pilot project was conducted in 1981 to determine the feasibility of detecting schools of capelin in inshore areas by aerial survey. This technique appears promising and expanded surveys using professional aerial survey personnel are planned for 1982.

One larval survey is now being conducted each year in an effort to estimate year-class strengths of capelin as 0-group fish. This survey has been conducted for 3 years but the first 2 years were largely unsuccessful because of vessel and weather problems. However, the cruises have permitted an evaluation of techniques and equipment and the 1981 survey will probably be considered the first in the time-series. By their nature, such surveys require a long time-series to test their results with estimates of adult stock size.

Because of the necessity of monitoring the current fisheries and providing biological advice to managers on total allowable catches, and so on, very little research on biology of capelin is being conducted, although many gaps in our knowledge exist. The exceptions to this are the studies planned in Trinity Bay, and studies on eggs and newly emerged larvae (Frank and Leggett 1981*a*, 1981*b*) now being conducted in Conception Bay by personnel from McGill University.

No studies are being conducted to test the effects of fluctuations of capelin abundance on the dynamics of cod or other predators. Such studies are attractive but require careful planning and large commitments of personnel and funds over a number of years. At present, extensive collections of stomachs of several predators (cod, Greenland halibut, American plaice, harp seals) of capelin are being accumulated and examined and these should improve our understanding of the time, place, and intensity of interactions between capelin and its predators.

7. Acknowledgements

I thank W.C. Leggett, G. Lilly, G.H. Winters, and an anonymous reviewer for critically reviewing the manuscript.

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Capelin and seabirds in the northwest Atlantic

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1. Abstract

Capelin (*Mallotus villosus*) are central to the food webs of seabirds, marine mammals, and fish in Newfoundland waters. The area of Witless Bay, southeast Newfoundland (*ca.* 47°14′N 52°46′W) contains the largest breeding concentration of seabirds in Canada and includes *ca.* 1.25 million individuals whose principal diet is fish; these consume *ca.* 7300 t of capelin during the major part of the breeding season, 1 June – 15 August. The annual capelin consumption by all seabirds in Newfoundland waters is *ca.* 250 000 t, of the same order of magnitude as that by seals and whales, and one-tenth that of Atlantic cod (*Gadus morhua*). The proportion of the total Newfoundland capelin biomass consumed by these predators is not known. However the birds' requirement for prey at locally high densities for efficient foraging, and the limitations imposed by their inability to dive deeply and by their need to forage close to their colonies, suggest that only part of this total biomass is available to them.

Capelin were the principal prey brought to Atlantic Puffin (*Fratercula arctica*) chicks on Great Island, Witless Bay, in 1968–69, but the young birds were fed mainly on small gadids in 1981. In 1981, chicks received an average of only 13.47 g food/day (against 44.64 g in 1968–69), fledged at an average body weight of 217.0 g (against 261.6 g), and fledging success was only 45.0% (against 60.3%). It is concluded that capelin form an essential part of the diet of young puffins in eastern Newfoundland, and that there is no alternative prey, of comparable size, abundance, and nutritional value available to the birds within range of Witless Bay. The responses of puffins and other seabirds to scarcities of key food species elsewhere are reviewed. In most cases the more specialized seabird species have no acceptable alternative to their principal prey.

The fishery for capelin which has developed off Newfoundland since 1971 therefore places seabirds and people in potential competition for a common resource. It is not clear to what extent the scarcity of capelin off Witless Bay in 1981, and a failure in capelin stock recruitment on the Grand Banks in 1978, was an effect of the fishery and/or natural environmental factors. However, any serious decline in the Newfoundland capelin stocks would have adverse effects on the principal predators. A program to monitor the populations of these predators would provide an indication of the condition of the capelin stocks and give advance warning of population declines. The management of this fishery should proceed cautiously until the relationships between the capelin and its predators are better understood.

2. Résumé

Le capelan (*Mallotus villosus*) occupe une place clé dans la chaîne trophique des oiseaux aquatiques, des mammifères marins et des poissons des eaux de Terre-Neuve. La région de Witless Bay, au sud-est de Terre-Neuve (environ 47°14′N 52°46′O), abrite la plus grande concentration d'oiseaux aquatiques nidificateurs du Canada, dont près de 1,25 million de sujets qui se nourrissent principalement de poissons; ils consomment près de 7300 t de capelan durant la majeure partie de la période de nidification qui s'étend du 1er juin au 15 août. La consommation annuelle de capelan par tous les oiseaux aquatiques des eaux de Terre-Neuve se chiffre à environ 250 000 t, soit le même ordre de grandeur que celle des phoques et des baleines, et le dixième de celle de la morue (*Gadus morhua*). La proportion de la biomasse totale de capelan de Terre-Neuve absorbée par ces prédateurs n'est pas connue. Cependant, le fait que leurs proies doivent atteindre des densités localement élevées pour que les oiseaux pêchent efficacement, qu'ils soient limités par leur incapacité à plonger en profondeur ou par la nécessité de pêcher près de leurs colonies, laisse supposer que seule une partie de cette biomasse totale leur est accessible.

Le capelan a été la principale proie apportée à de jeunes Macareux arctiques (*Fratercula arctica*), à Great Island, Witless Bay, en 1968–1969, alors qu'en 1981, les jeunes oiseaux ont été nourris principalement de petits gadidés. En 1981, les oisillons n'ont reçu en moyenne que 13,47 g de nourriture par jour (comparativement à 44,64 g en 1968–1969); ils étaient en mesure de voler avec un poids corporel moyen de 217,0 g (contre 261,6 g), avec un succès d'envol de 45,0 % (contre 60,3 %). Ces observations ont amené à conclure que le capelan forme un élément essentiel du régime des jeunes macareux, à l'est de Terre-Neuve, et que ces oiseaux ne disposent d'aucune autre proie de taille, d'abondance et de qualité nutritive comparables, aux alentours de Witless Bay. Les auteurs revoient les réactions des macareux et d'autres oiseaux aquatiques à la rareté d'espèces alimentaires clés ailleurs. Dans la plupart des cas, les espèces plus particulières d'oiseaux aquatiques ne disposent d'aucune autre nourriture acceptable pour remplacer leur proie principale.

La pêche au capelan qui s'est développée au large de Terre-Neuve depuis 1971 a créé une rivalité entre les oiseaux aquatiques et l'homme pour le partage de cette ressource. On n'a pu déterminer dans quelle mesure la rareté du capelan au large de Witless Bay en 1981 et le recrutement insuffisant des stocks à Grand Banks en 1978

résultent de la pêche et/ou de facteurs écologiques naturels. Toutefois, toute baisse importante des stocks de capelan de Terre-Neuve serait préjudiciable aux principaux prédateurs. Un programme de surveillance des populations de prédateurs donnerait une indication de l'état des stocks de capelan et signalerait à l'avance toute baisse de population. Cette pêche devrait être aménagée avec précaution jusqu'à ce que les relations entre le capelan et ses prédateurs soient mieux connues.

3. Introduction

There are several marine ecosystems in which certain animal species stand out as being central to the food webs of many higher predators. In the Canadian High Arctic, for example, the principal trophic pathways in ice-edge habitats pass from the phytoplankton on the underside of the ice via the epontic and free-swimming copepods and amphipods, to the arctic cod (*Boreogadus saida*), before branching out again to seabirds, whales, and seals (Dunbar 1981, Bradstreet and Cross 1982). In Newfoundland waters the capelin (*Mallotus villosus*), a small smelt, occupies a comparable, central position (Winters and Carscadden 1978; Carscadden *et al.* 1982; Carscadden, this volume; see below), as does the northern anchovy (*Engraulis mordax*) off Oregon (Wiens and Scott 1975). The chain may be even simpler than this, and run from the phytoplankton directly to the central prey species (anchovetas [*Engraulis ringens*] in Peru and euphausiid krill [*Euphausia superba*] in the Antarctic), and then to the predators (e.g. Murphy 1936, Mauchline and Fisher 1969, Schaefer 1970). Sometimes a small group of species has this central role: sprat (*Sprattus sprattus*), sandlance (*Ammodytes* spp.), and young Atlantic herring (*Clupea harengus*) for British seabirds (Pearson 1968, Harris and Hislop 1978), or pilchard (*Sardinops ocellata*) and anchovies (*Engraulis capensis*) for those in South Africa (Crawford and Shelton 1978).

In recent years most of these central prey species have become the actual or proposed targets for intensive fisheries. This raises a number of questions about the fate of the higher predators which depend on them. How much of the stock of the prey do the predators require, and how much is harvested in the fishery? Can the two coexist? If not, to what extent are the predators able to adjust their feeding habits to alternative prey? In fact, *are* there any acceptable alternative prey species available to them? The object of this paper is to examine these questions with reference to the interactions of capelin, seabirds and other predators, and the fishery, off Newfoundland.

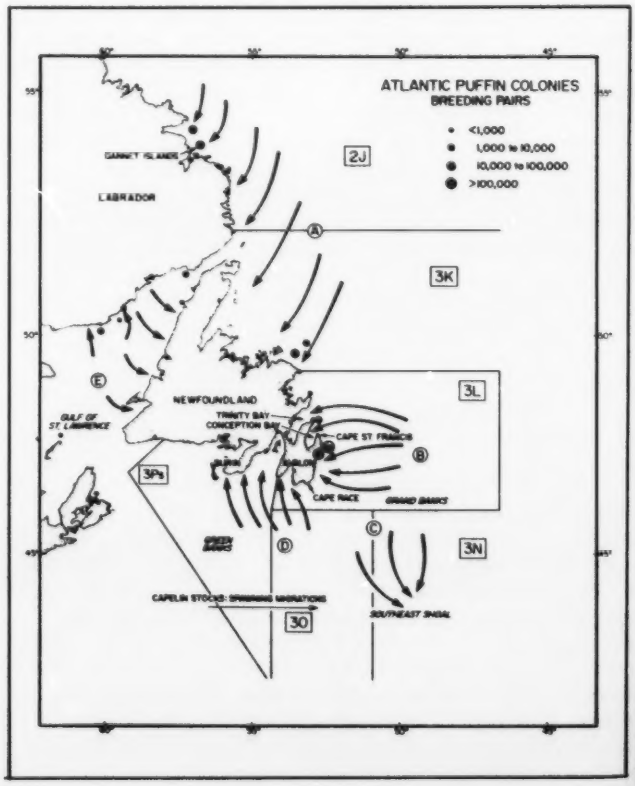
4. The distribution and habits of capelin

Capelin occur in the low arctic waters of both the North Atlantic and the North Pacific (Jangaard 1974). In the Atlantic the species is especially abundant off Newfoundland, southern Greenland, and Iceland, and in the Barents Sea (Leim and Scott 1966, Jangaard 1974). There are several discrete populations off eastern Canada (Carscadden, this volume; see also Fig. 1). Stock A occurs on the banks off southeast Labrador and northeast Newfoundland (International Commission for the Northwest Atlantic Fishery/Northwest Atlantic Fisheries Organization [ICNAF/NAFO] subareas 2J + 3K), and spawns on beaches along those coasts. Stock B, on the northern Grand Banks (3L), spawns on the beaches of eastern Newfoundland from Cape Freels to Cape Race. Stock C winters on the northern Grand Banks and spawns on the shallow Southeast Shoal of the Bank (3N0). Stock D, from the western Grand Banks and Green Bank (3Ps), spawns on beaches from the southern Avalon Peninsula to the Burin Peninsula. Stock E is confined to the Gulf of St. Lawrence. We are concerned primarily with stocks A–C in this paper.

Spawning occurs in June and July, earlier in southern Newfoundland than in Labrador (Templeman 1948; Jangaard 1974; Carscadden, this volume). The spawning schools consist mainly of 3–5 year-old fish, though younger fish may also migrate inshore at this season. Most of the adults die after they have spawned. The remainder, along with the immature fish, withdraw offshore again from August onwards, though part of stock A apparently winters off northeast Newfoundland. A small population also winters in deep water in Trinity Bay, southeast Newfoundland (Winters 1970).

In Newfoundland waters capelin are important to many higher predators (Jangaard 1974, Winters and Carscadden 1978, Akenhead *et al.* 1982). They are taken in large numbers by Atlantic cod (*Gadus morhua*) (and thus are of indirect importance to the many predators which feed on

Figure 1
Distributions of Atlantic puffins (*Fratercula arctica*) and capelin in Newfoundland and Labrador (after Brown *et al.* 1975 and Carscadden, this volume, respectively). The letters (A, B, C, D, E) refer to capelin stocks. The codes (2J, 3K, 3L, 3N, 3O, 3Ps) refer to ICNAF/NAFO subareas (ICNAF/NAFO 1963–83). W identifies the major colonies of puffins and other seabirds in Witless Bay, Newfoundland (see Table 1 and the text)



cod), Greenland halibut (*Reinhardtius hippoglossoides*), American plaice (*Hippoglossoides platessoides*), and other demersal fish; by Atlantic salmon (*Salmo salar*), and bluefin tuna (*Thunnus thynnus*); by harp seals (*Pagophilus groenlandicus*), and fin, sei, and minke whales (*Balaenoptera physalus*), (*B. borealis*), and (*B. acutorostrata*); by short-finned squid (*Illex illecebrosus*); and by many seabirds.

5. The importance of capelin to seabirds in Newfoundland

Newfoundland and Labrador support a large population of breeding seabirds. The largest concentration, in Canada as well as Newfoundland, breeds on Gull, Green, and Great islands in Witless Bay on the Avalon Peninsula, *ca.* 47°14′N 52°46′W (Nettleship 1980, see Fig. 1). The

Table 1
Population sizes of the principal seabird species breeding in Witless Bay, Newfoundland, and estimates of their consumption of capelin over the 45-day period 1 July – 15 August. Estimates of sizes of the breeding populations are from Nettleship (1980); those for non-breeding subadults were calculated by using productivity figures from Maunder and Threlfall (1972), Nettleship (1972), Pierotti (1979), and survival rates from Coulson and White (1959), Coulson (1968), Kadlec and Drury (1968), Birkhead and Hudson (in press)*

	Herring Gull	Black-legged Kittiwake	Common Murre	Atlantic Puffin	Totals
No. breeding adults (*A*)	**13 700**	**84 000**	**156 000**	**450 000**	
No. eggs laid (*X* clutch size)	17 125 (2.5)	77 700 (1.85)	78 000 (1)	225 000 (1)	
No. chicks hatched (hatching, %)	12 673 (74%)	55 944 (72%)	66 300 (85%)	157 500 (70%)	
No. chicks fledged (fledging, %)	9 885 (78%)	42 517 (76%)	56 670 (90%)	102 375 (65%)	
Average no. chicks present (*B*)	**11 000**	**49 000**	**63 000**	**125 000**	
No. non-breeding subadults					
1-year-olds	3 022	33 588	29 835	51 000	
2-year-olds }	3 425	28 550	22 376	38 250	
3-year-olds }		—	19 020	30 600	
4-year-olds	—	—	16 167	26 010	
Total subadults (*C*)	**6 447**	**62 138**	**87 398**	**145 860**	
Total no. birds	***ca.* 31 000**	***ca.* 195 000**	***ca.* 306 000**	***ca.* 721 000**	
Food consumption					
a. adults	(@ 400 g × 75 d × *A*)	(@ 50 g × 75 d × *A*)	(@ 200 g × 75 d × *A*)	(@ 100 g × 75 d × *A*)	
(% capelin)	411 t (30%)	315 t (40%)	2340 t (90%)	3375 t (90%)	
b. chicks	(@ 200 g × 15 d × *B*) (@ 400 g × 30 d × *B*)	(@ 50 g × 45 d × *B*)	(@ 27 g × 20 d × *B*) (@ 54 g × 25 d × *B*)	(@ 52 g × 45 d × *B*)	
(% capelin)	165 t (30%)	110 t (90%)	119 t (90%)	292 t (90%)	
c. subadults	(@ 400 g × 45 d × *C*)	(@ 50 g × 45 d × *C*)	(@ 200 g × 45 d × *C*)	(@ 100 g × 45 d × *C*)	
(% capelin)	116 t (30%)	140 t (40%)	787 t (90%)	656 t (90%)	
Total food consumption	692 t	565 t	3246 t	4323 t	8826 t
Total capelin consumption	208 t	281 t	2921 t	3891 t	7301 t

*The adults of all four species are present on the Witless Bay colonies all through June as well as from 1 July – 15 August. These would require an additional 2576 t of food (Herring Gull: 164 t; kittiwake 126 t; murre: 936 t; puffin 1350 t) for this additional 30-day period, or 2152 t of capelin if the suggested ratios for percent capelin also apply to the beginning of the season.

Five other seabird species breed in the Witless Bay colonies (Nettleship 1980): *ca.* 780 000 pairs of the planktivorous Leach's Storm Petrel, and well under 1000 pairs each of the wholly or partly fish-eating Great Black-backed Gull, Thick-billed Murre, Razorbill, and Black Guillemot. These will not be taken into consideration in the present paper.

Table 2
The occurrence of various classes of food items (%) in the diets of Herring Gulls (HG), Black-legged Kittiwakes (BLK), Common and Thick-billed murres (CM,TBM), and Greater Shearwaters (GSH) in eastern Newfoundland. *n* = the number of samples on which the percentages are based. Samples from Witless Bay (WB) refer to breeding birds; those from eastern Newfoundland (ENFLD), eastern Grand Bank (EGB), Placentia Bay (PB), and Notre Dame Bay (NDB) to non-breeders. The percentages for Herring Gulls, Kittiwakes, and murres refer to the number of meals (WB) or stomachs (ENFLD) in which the item in question was the *sole* or *principal* constituent. Greater Shearwater percentages refer to every stomach in which the item occurred, and so the sum of the percentages exceeds 100%. Data from Rees (1961), Tuck (1961), Maunder (1971), Brown *et al.* (1979), Mahoney (1979), Pierotti (1979)

Area:	WB						ENFLD		EGB	PB	NDB
Species:	HG*			BLK†	CM		CM	TBM	GSH		
Season:	June–July			June–August	June–July		Winter		June	June	September
Year:	1976	1977	1978	1970	1977	1978	—	—	1961	1978	1975
Item											
Capelin	34.4	26.4	30.8	40.8	92.9	94.1	91.7	93.1	21.0	60.0	100.0
Other fish	5.7	6.2	3.8	20.9	2.2	2.9	7.0	5.9	0	0	0
Squid	0.8	14.5	10.1	0.3	4.9	0	0	0	23.7	50.0	7.7
Crustaceans	0	0	0	1.4	0	0	0	0	15.8	10.0	7.7
Birds	46.5	18.5	20.0	0	0	0	0	0	0	0	0
Other }	12.5	27.9	28.5	6.0	0	2.9	1.3	1.0	0	0	0
Offal–garbage }		6.4	7.3	30.6	0	0	0	0	42.1	0	0
No.	494	1200	891	265	372	183	44	614	38	20	13

*"Birds" refers to young Atlantic Puffins or adult Leach's Storm Petrels; "Other" consists mainly of littoral molluscs and barnacles. See Table 3 for the foods brought to young Atlantic Puffins.

†18.9% of the "other fish" in 1970 were sandlance; however capelin was the principal food brought to the chicks in 1970 and also 1969 (Maunder 1971, Maunder and Threlfall 1972).

Table 3
Comparison of breeding performance in Atlantic Puffins in Witless Bay, Newfoundland, in 1968–69 and 1981.[a]

Measure	1968–69[b]		1981[b]		χ^2 or t	P[c]
Fledging success	60.3% (126/209)		45.0% (45/100)		$\chi^2 = 29.37$	<0.001
Chick mortality						
(a) found dead in burrow (i.e. starvation)	15.7% (13/83)		44.4% (24/54)[d]		$\chi^2 = 13.75$	<0.001
(b) disappeared prematurely (i.e. gull predation/ early departure)	84.3% (70/83)		55.6% (30/54)[d]		$\chi^2 = 13.75$	<0.001
Chick condition at fledging	(n = 126)		(n = 45)			
(a) body weight, g	261.6 ± 34.07 (159–323)		217.0 ± 38.22 (145–276)		$t = 6.91$	<0.001
(b) wing length, mm	142.1 ± 14.19 (127–154)		140.0 ± 6.36 (126–152)		$t = 1.42$	NS[f]
Chick diet	n		n			
(a) meal size, g	155	12.4 ± 5.33	101	5.86 ± 4.95	$t = 10.02$	<0.001
(b) composition:	208 (1969)		101			
capelin	175	84.13%	13	12.9%	$\chi^2 = 144.92$	<0.001
immature *Gadus*	7	3.36%	65	64.3%	$\chi^2 = 141.51$	<0.001
sandlance	26	12.50%	14	13.9%	$\chi^2 = 0.11$	NS
total fish	208	100.00%	92	91.1%	$\chi^2 = 19.09$	<0.001
invertebrate	0	0.00%	9	8.9%	$\chi^2 = 19.09$	<0.001
(c) $\bar{x}$ feeding rate (meals/chick/d)[e]	17 (1969)	3.6 ± 1.08	20	2.3 ± 2.65	$t = 2.01$	≈0.05
(d) estimated $\bar{x}$ chick food/c/d, g [(a) · (c)]	17	44.64	20	13.47		

[a]Same study plots and habitats (slope) used in 1981 as base years 1968–69.
[b]1968–69 was prior to international capelin fishery; 1981 was 9 years after beginning of fishery. 1981 was 3rd consecutive year of apparent capelin spawning failures in SE Newfoundland waters.
[c]Statistical tests used (from Sokal and Rohlf 1969) are either chi-square (χ^2) from 2 × 2 contingency tables testing the significance of the difference between the proportions indicated, or Student's t-distribution.
[d]Fate of one chick uncertain though known *not* to have fledged.
[e]Chicks watched for 3 days and therefore 1969 = 51 chick-days, and 1981 = 60 chick-days.
[f]NS, $P > 0.05$.

ca. 2.2 million individuals there include, in descending order of abundance, Leach's Storm-petrels (*Oceanodroma leucorhoa*), Atlantic Puffins (*Fratercula arctica*), Common Murres (*Uria aalge*), Black-legged Kittiwakes (*Rissa tridactyla*) and Herring Gulls (*Larus argentatus*), along with smaller numbers of Thick-billed Murres (*Uria lomvia*), Razorbills (*Alca torda*), Black Guillemots (*Cepphus grylle*), Great Black-backed Gulls (*Larus marinus*), and Northern Fulmars (*Fulmarus glacialis*) (Table 1).

Of these species, Leach's Storm-petrel is planktivorous (e.g. Palmer 1962). The remainder are all, to some extent, fish-eaters. Tables 2 and 3 show that murres and puffins, the dominant alcids, feed almost entirely on fish and the two gulls, kittiwake and Herring Gull, also take fish to a lesser degree. Overall, the tables show that capelin are the dominant fish in the diets of Witless Bay seabirds.

Table 1 attempts to quantify these diets during the central part of the breeding season. During 1 July – 15 August, adult birds, their growing chicks at the nest sites, and subadult birds are all present at the colony. The adults are also there earlier, during the incubation period (roughly 1–30 June), but subadult seabirds tend to arrive later in the season (e.g. Salomonsen 1967) and for present purposes we assume that they are absent before 1 July. The estimates of food consumption in the table are necessarily speculative but we believe that they are reasonably accurate — more so for the specialist murres and puffins than for the gulls, generalist feeders — and consistent with estimates for murre colonies elsewhere (Table 4). We conclude that the Witless Bay seabird population consumes *ca.* 8830 t of food during this 75-day period, of which *ca.* 7300 t are capelin. Birds are at the colonies for at least 2 months before, and 1 month after this central period. However we hesitate to extrapolate our estimates further, partly for lack of information about the birds' diets at these times, and partly because the capelin are farther offshore then, and may be less accessible (Jangaard 1974).

Because the distributions of the principal colonies of puffins and other seabirds coincide with those of spawning capelin (Fig. 1; see also Nettleship 1973, 1977, 1980; Brown *et al.* 1975), it is reasonable to extrapolate our estimates for Witless Bay to cover the whole Newfoundland seabird population for the period 1 June – 15 August. There is not enough information to do this for Herring Gulls, but we estimate (Table 4) that the murres, puffins, and kittiwakes combined take a total of *ca.* 25 600 t of capelin, of which *ca.* 17 300 t comes from stock A (subareas 2J and 3K) and *ca.* 7900 t from stock B (subarea 3L, including Witless Bay). These estimates take partial account of consumption by the subadults of these species. However, they do not include consumption by the large numbers of non-breeding Greater and Sooty shearwaters (*Puffinus gravis* and *P. griseus*), migrants from the southern hemisphere, which are widely distributed in subareas 2J + 3KLNOPs during this period (Brown *et al.* 1975). Too little is known about the diets or population sizes of either species to estimate their consumption of capelin with any accuracy, but we conclude from the calculations in Table 4 that, as a first approximation, it may be of the order of 25 000 t. Finally, large numbers of seabirds feed on capelin while they are wintering off Newfoundland; most notably *ca.* 4 million Thick-billed Murres from Greenland and the Canadian Arctic, and many of the *ca.* 1 million Common Murres which breed in Newfoundland and Labrador, both capelin-feeders in win-

Table 4

A preliminary estimate of food consumption by breeding Black-legged Kittiwakes, Common Murres, and Atlantic Puffins in southeast Labrador and eastern Newfoundland in the season 1 June – 15 August. NAFO subareas 2J and 3K = capelin stock A, 3L = stock B, and 3Ps = stock D (Carscadden, this volume). Numbers of breeding adults from Nettleship (1980), supplemented by Brown *et al.* (1975); subadults and chicks calculated from the adult–subadult–chick ratios for the Witless Bay colonies (Table 1). Feeding rates and periods, and capelin consumption, also from Table 1

Capelin stock:		**A**		**A**		**B**		**D**		
Subarea:		**2J**		**3K**		**3L**		**3Ps**		
		No. birds	**Food, t**	**No. birds**	**Food, t**	**No. birds**	**Food, t**	**No. birds**	**Food, t**	**Totals**
Kittiwake	(1 ad./0.74 subadults/ 0.58 chicks)									
Adults	(75 d @ 50 g/d)	100	0.4	6000	22.5	105060	394.0	22944	86.0	
Subadults	(45 d @ 50 g/d)	74	0.2	4440	10.0	77744	174.9	16978	38.2	
Chicks	(45 d @ 50 g/d)	58	0.1	3480	7.8	60935	137.1	13307	29.9	
Total		232	0.7	13920	40.3	243739	706.0	53229	154.1	
Common Murre	(1 ad./0.56 subadults/ 0.40 chicks)									
Adults	(75 d @ 200 g/d)	68200	1023.0	799200	11988.0	157690	2369.4	20140	302.1	
Subadults	(45 d @ 200 g/d)	38192	343.7	447552	4028.0	88458	796.1	11278	101.5	
Chicks	(20 d @ 27 g/d) (25 d @ 54 g/d)	27280	14.7 36.8	319680	172.6 431.6	63184	34.1 85.3	8056	4.3 10.9	
Total		133672	1418.2	1566432	16620.3	309602	3824.9	39474	418.8	
Atlantic Puffin	(1 ad./0.32 subadults/ 0.28 chicks)									
Adults	(75 d @ 100 g/d)	91730	688.0	25000	187.5	471840	3538.8	0	0	
Subadults	(45 d @ 100 g/d)	29354	132.1	8000	36.0	150989	679.4	0	0	
Chicks	(45 d @ 52 g/d)	25684	60.1	7000	16.4	132115	309.1	0	0	
Total		146768	880.2	40000	239.9	754944	4527.3	0	0	
Total food, t			2291		16900		9058		573	28822
Total capelin consumption			2069		15195		7887		458	25609

NOTE: — Additional species:

Herring Gull: the size of the Newfoundland population is not known, but Table 1 estimates the capelin consumption for this period in Witless Bay as *ca.* 208 t.

Shearwaters: 5–10 million Greater Shearwaters breed in the South Atlantic and winter in the North Atlantic in June–October, along with large numbers of Sooty Shearwaters – initially off eastern North America (Rowan 1952; Phillips 1963; Voous and Wattel 1963; Brown *et al.* 1975, 1981; Bourne 1980). For present purposes we will assume that 3 million shearwaters are present 1 June – 15 August in 2J + 3KLNOPs and that each bird, weighing 800 g, consumes 175 g/d (based on the 200–250 g/d of 900 g Common Murres, Sanford and Harris [1967], Swennen and Duiven [1977]), half squid and half capelin by weight (Table 2). Total food = 39400 t; total capelin = 19700 t. Alternatively, we follow Morejohn *et al.* (1978) in assuming that the calorific content of the squid is 5.1 kJ/g (wet), and that a shearwater can assimilate 80% of the calorific content of its food and requires, resting, 271 kcal/d (1135 kJ/d). With capelin @ 4.2–4.5 kJ/g (Jenkins [1974]; Montevecchi and Porter [1980]; samples from summer, eastern Newfoundland) the birds consume 70–76000 t of food (35–38000 t of capelin) in a 75-d period. With capelin @ 17.8 kJ/g (M.S.W. Bradstreet, in prep; summer, southeast Labrador), total consumption would be *ca.* 18000 t if 100% of the diet was capelin, and progressively less with increasing proportions of squid. However the lack of definite information on shearwater numbers, diets, and metabolic rates makes these figures first approximations only.

Comparative data: Wiens and Scott (1975), using an energy-flow model, estimate that 3–4 million Sooty Shearwaters consume 30717 t of food (80% of it northern anchovies @ 4.3 kJ/g) in a 2.5–3-month period off Oregon. On the same model they estimate that 239800 breeding Common Murres consume 6409 t (mainly anchovies) during a 4-month breeding season, and 21142 t over the whole year. Other estimates for Common and/or Thick-billed murres, based on daily consumption rates over a 4-month breeding season, are 4300 t (Wiens and Scott 1975), 25000 t (Uspenski 1956: 2 million birds in Novaya Zemlya) and 49000 t (Swartz 1966: 157000 birds in the Bering Sea).

More generally, Wiens and Scott (1975) estimate that seabirds take *ca.* 20% of the production of pelagic fish in the neritic zone (up to 37 km offshore) off Oregon. Furness (1978) estimates *ca.* 29% within a 45-km radius of Shetland, and Furness and Cooper (1982) give a figure of *ca.* 30% within 50 km of Saldanha Bay, South Africa. Schaefer (1970) estimates *ca.* 20% for the seabirds of Peru.

ter (Tuck 1961, Gaston 1980). We suggest (Table 5), again as a first approximation, that the breeding and non-breeding seabirds take a total of *ca.* 250000 t of capelin from Newfoundland waters in the course of the year.

The seabirds' annual consumption of capelin in subareas 2J + 3KLNOPs is therefore of the same order of magnitude as consumption in those areas in the 1970s by the fishery at its peak, by harp seals, and by fin and minke whales; it is about a tenth the consumption calculated for Atlantic cod in the same period and subareas (Winters and Carscadden 1978, see also Table 5 and Fig. 2). It is difficult to view these figures in the wider perspective of the absolute biomass of capelin in these subareas, since the estimates of consumption given by Winters and Carscadden (1978) and Table 5 are minima which take no account of the biomass of fish left *unconsumed*. Population estimates based on acoustic surveys suggest that the peak biomass of capelin in subareas 2J + 3KLNOPs in 1976 was *ca.* 10.3 million metric tons (using the higher estimate in Table 5); the fishery took only *ca.* 3.5% of this, against *ca.* 37% by all natural predators combined, including only *ca.* 2.4% by the seabirds. On the other hand the seabirds alone would have required *ca.* 23% and the natural predators *ca.* 350% of the *ca.* 1.1 million metric tons estimated for 1979. The results of acoustic surveys vary with the method used, and they are more reliable as *relative* indices of annual changes in capelin numbers than as *absolute* estimates of capelin biomass (Carscadden, this volume). Even so, the figures suggest that the present low level of capelin biomass may be imposing limits on the populations of the higher predators.

However, it is important to emphasize that the significant index for the predators is probably not so much the overall size of the capelin stock in a given subarea, as the *local* density of the fish within relatively small areas. It is this which determines the foraging efficiency of the predators. Brodie *et al.* (1978) have calculated that a fin whale feeding on euphausiids on the Scotian Shelf cannot meet its daily energetic requirements at a prey density of only 0.1 g/m^3, the average density of euphausiids in that area; it must instead search for "patches" of euphausiids as dense as 17.5 g/m^3 or higher. The use which seabirds make of "fronts," tidals upwellings and similar oceanographic systems which concentrate their prey suggests that their foraging is also determined by local concentrations rather than overall abundance (Nettleship 1977, Brown 1980). Off Novaya Zemlya the Dovekie (*Alle alle*), a small, diving, planktivorous alcid, can in theory reduce the time it spends foraging underwater by two-thirds, if it hunts in areas of maximum rather than average prey density, and the feeding birds do indeed concentrate in such areas (Zelickman and Golovkin 1972, Brown 1981). It is not possible to say precisely what such a reduction in foraging time means in energetic terms, but there can be little doubt that it represents a significant saving. The energetic costs of swimming transport in a Mallard (*Anas platyrhynchos*) are about six times greater than those of flying (Prange and Schmidt-Nielsen 1970). It is likely that fish-eating alcids like murres and puffins can also reduce their energetic costs by foraging on locally dense concentrations of capelin.

Whether the index of capelin biomass is local or general, seabirds are further limited in their access to the resource by restrictions that do not apply to the other natural predators. Seabirds breed only on land, and so the

Figure 2
Annual landings of capelin in eastern Newfoundland (metric ton × 10^3, round, wet). The combined catches from areas 2 and 3 (mainly 2L + 3KLNOPs) are listed under "E.NFLD." "3L Offshore" and "Inshore" indicate, respectively, the catches by foreign and by Newfoundland vessels in subarea 3L, and "3L Southern Shore" those taken inshore between Cape St. Francis and Trepassey (and including Witless Bay). 3L catches refer primarily to capelin stock B, though part of the offshore catch may include fish from stock C (Carscadden, this volume). Data from ICNAF/NAFO (1963-83) and Anon. (1982); the data for 1981 are provisional.

Note that part of the "inshore" catch in 3L in 1974 may have been taken by large Newfoundland vessels operating *offshore*; the offshore catch in 3L (and in E.NFLD) in 1975 may have been underestimated by *ca.* 25 000 t (Carscadden, this volume).

Since 1979 the inshore fishery in 3L has concentrated on the harvesting of mature female capelin for their roes (Anon. 1982). As a consequence, males and unripe or substandard females are rejected and do not appear in the landings statistics (Rowe and Collins 1982). The actual catch inshore in 1979–81 may therefore have been double that shown here

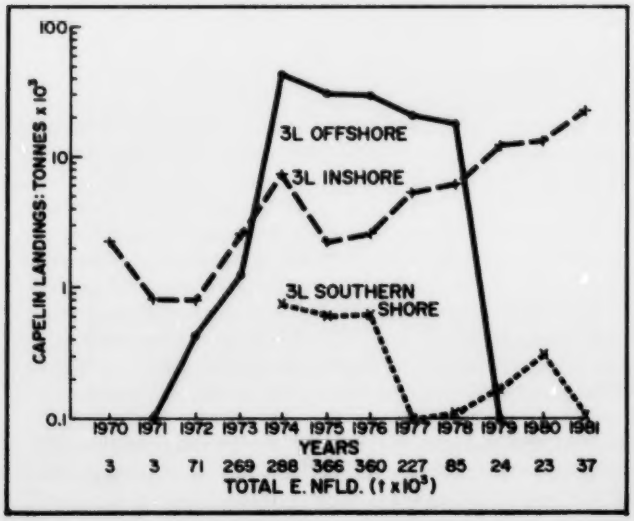


Table 5
Consumption, in metric tons, of capelin by seabirds, other predators and people off eastern Newfoundland

Annual consumption by seabirds in subareas 2J + 3KLNOPs	
4 million Thick-billed Murres, November–March @ 200 g/d (Gaston 1980)	108 000
1.6 million Common Murres, January–December @ 200 g/d (from Brown *et al.* 1975 and Tables 1,4)	105 000*
0.8 million Atlantic Puffins, April–October @ 100 g/d (from Brown *et al.* 1975 and Tables 1,4)	15 000
3 million Greater and Sooty shearwaters, June–August (Table 4)	25 000
Total	*ca.* 250 000

Annual consumption in subareas 2J + 3KLNPOs (based on Winters and Carscadden 1978; Carscadden, this volume)

Predator	*ca.* 1955–57	early 1970s	Exploitable surplus†
Seabirds	250 000	250 000	—
Harp seals (*Pagophilus groenlandicus*)	432 000	300 000	132 000
Fin whales	360 000	250 000	110 000
Minke whales	35 000	20 000	15 000
Atlantic cod	3 970 000	3 000 000	970 000
Totals	5 047 000	3 820 000	1 227 000
Peak capelin catch, 1975, areas 2,3			365 971‡
Capelin catch, 1981, areas 2,3			36 678‡
Estimated absolute biomass 1976§		10 344 000	
Estimated absolute biomass 1979§		1 104 000	

The requirement for capelin by seabirds breeding in Witless Bay (1 June – 15 August) in relation to the biomass of mature, 3–5 year-old fish potentially available to them at increasing distances from the colony

Foraging radius from Witless Bay, km	Local capelin biomass**	Birds' requirement (= *ca.* 7300 t: as % of local biomass)
5	4 450	164
20	17 800	41
50	44 500	16
100	89 000	8

*It is assumed that the whole population winters off Newfoundland. However Common Murres also occur in winter as far south as Georges Bank, outside the range of capelin (e.g. Powers and Rumage 1978); if these are Newfoundland birds, the actual capelin consumption from November–March will, to an unknown degree, be less than that estimated here.

†Based on the estimated biomass of capelin left unconsumed by the decline in predator populations between the late 1950s and early 1970s; no estimates of changes in seabird populations available.

‡Probably too low: see caption to Figure 2.

§1976 and 1979 are, respectively, the peak and minimum biomasses for 2J + 3KL, extrapolated to cover 3NOPs as well following the calculations of Winters and Carscadden (1978) for cod (Akenhead *et al.* 1982). Another method of estimating biomass gives 1 890 000 t (1975, peak) and 495 000 t (1979). Both methods are more reliable as relative indices of year-to-year changes than absolute values of population size (Carscadden, this volume).

**The total biomass of capelin projected for 3L in 1981 was *ca.* 300 000 t (NAFO 1981). In the absence of a finer-scale analysis of distribution, we here assume that this biomass was evenly distributed along the *ca.* 800 km of shoreline in the subarea @ 445 t/km. However the catch statistics (Anon. 1982) suggest that this was not so and that capelin densities were lower than average in the Witless Bay area. In Trinity and Conception bays in 1981, 19 682 t of fish were caught (44 t/km or 46 t per licensed fisherperson), against only 66 t on the southern shore (0.4 t/km or 2.5 t/fisherperson).

breeding birds have access only to that proportion of the biomass that is within economical foraging range of their colonies. These ranges vary widely between species and colonies and may change rapidly, depending on the availability of prey (e.g. Tuck and Squires 1955, Nettleship and Gaston 1978, Gaston and Nettleship 1981). Their outer limits become crucial during the chick-rearing period, when the chick must receive a quantitatively and qualitatively sufficient daily intake of food to sustain its rapid growth. The foraging parents are further limited to a maximum 16 h day-length (Civil Twilight) at the latitude of Witless Bay because Common Murres, at least, are unable to pursue fish at night (Sanford and Harris 1967).

The actual foraging ranges of Witless Bay seabirds are not known with any certainty, but puffins and murres are regularly taken in gill nets set along the coast of the Avalon Peninsula at least 20 km from the colony (Piatt *et al.*, this volume). This suggests that the birds may travel quite far, though there is no indication of the foraging ranges of parents actually foraging for their young. Observations elsewhere suggest that most seabirds forage within a 35–50 km radius of their colonies (e.g. Wiens and Scott 1975, Furness 1978, Furness and Cooper 1982, see also Table 4). A Witless Bay puffin, with a flight speed of *ca.* 50 km/h (Pennycuick 1969: Fig. 8), could thus, in theory, have access to capelin of stock B along the entire length of the eastern Avalon Peninsula, from Cape St. Francis to Cape Race, in an hour's flight. If the fish were present at the depths and local concentrations suitable for efficient foraging, it could meet its food requirements from the biomass of capelin within 20–50 km of the colony (Table 5*c*). On the other hand, the fish of stock C on the Southeast Shoal offshore, *ca.* 370 km away from Witless Bay, would almost certainly be inaccessible to it. The only seabirds commonly seen out there during the capelin spawning season are the non-breeding shearwaters (Brown *et al.* 1975; R.G.B. Brown, in prep.).

The seabirds' access to their prey is also limited by their diving abilities; unlike competing predators, they cannot stay under water for long periods. Kittiwakes and Herring Gulls cannot submerge deeper than their own body length. Shearwaters may stay under for *ca.* 12–30 s and reach a depth of *ca.* 20 m (Brown *et al.* 1978, 1981; Skira 1979). The specialized alcids are more efficient divers, however. Common and Thick-billed murres have been recorded as diving for up to 140 and 192 s, respectively (Scott 1973, Bradstreet 1983), and the former will feed on the bottom at 60 m (Scott 1973). In the Witless Bay area, Common Murres are regularly taken in gill nets set at depths of 30–100 m but not in those at 6–10 m (Piatt *et al.*, this volume), which suggests that the species is a deep diver; however, the reverse is true of puffins. In general, most Newfoundland seabirds are limited to foraging in the top 30 m of the water column, and only the murres regularly go deeper. This would not limit foraging in the vicinity of the spawning beaches, where the capelin schools are at depths of 5–10 m or less (Templeman 1948). Shearwaters may be unable to reach fish spawning on the bottom offshore on the Southeast Shoal (minimum depth *ca.* 50 m), but they can probably take them there at shallower depths in mid water. On the other hand, the seabirds' access to capelin in deeper waters off Newfoundland is almost certainly limited by the depth of the schools. Acoustic surveys have shown that young, 1-year capelin stay close to the surface off Newfoundland during the summer, but that the larger, 2–3 year-old fish remain close to the bottom (*ca.* 100 m) during the daytime; they rise at night, but reach the surface only if the surface waters are cool (Devold 1970, Devold *et al.* 1972, Kovalyov and Kudrin 1973). Much of the capelin population is therefore too deep for any birds but murres to reach it during the daytime, and it is accessible to the other, diurnal and shallower-diving seabirds for only a limited period of daylight at dawn and dusk.

We therefore conclude that capelin are an extremely important prey for the more specialized seabird species breeding in Newfoundland, such as murres and puffins, and to a lesser extent generalist feeders such as kittiwakes and other gulls as well. They are also important to non-breeding shearwaters off Newfoundland in summer, and to migrant murres from the Arctic which winter on the Grand Banks. The seabirds' annual consumption, estimated very approximately at 250 000 t, is of the same order as that of the seals and whales, and also of the Newfoundland capelin fishery at its peak. However, it is difficult to relate this consumption to the overall size of the capelin biomass in Newfoundland waters, partly for lack of adequate information about the latter, but partly also because seabirds, like other higher marine predators, depend on *local* densities rather than overall biomass for foraging efficiency. The seabirds are further constrained by their limited diving abilities, and by the restrictions on their foraging ranges imposed by their need to breed on land. Taken together, these constraints mean that seabirds, and to some extent the other higher predators as well, have access to a smaller capelin population than is, in theory, available to them.

6. Alternatives to capelin in the diets of Newfoundland seabirds

The importance of capelin in the diets of Newfoundland seabirds is also demonstrated by the reduced breeding success of the birds in seasons when the fish are scarce or absent during the chick-rearing period.

In 1981 the Atlantic Puffins nesting on Gannet Islands, southeast Labrador (Fig. 1) bred successfully, feeding their young almost entirely on capelin (Birkhead and Nettleship 1982). This was not true of the birds on Great Island in Witless Bay. The principal fish in the chicks' diets at this colony in 1981 were young gadids (64.3%), supplemented by small numbers of sandlance (13.9%), capelin (12.9%), and invertebrates (8.9%) (Table 3). Only 45.0% of the chicks fledged, and 44.4% of those which failed to do so died of starvation in their burrows. This is in sharp contrast to the 1968 and 1969 breeding seasons at this colony, when the food brought to the chicks consisted entirely of fish: mainly capelin (84.1%), with smaller numbers of sandlance (12.5%) and a few gadids (3.4%). Sixty percent of the young birds fledged in these two seasons, and only 15.7% of those which failed to do so were found dead of starvation in their burrows; the remainder were probably taken by gulls (Nettleship 1972).

The weights of the young puffins which did fledge at Great Island in 1981 averaged only *ca.* 83% of those which fledged in 1968–69. The subsequent survival of seabird chicks is apparently correlated with their fledging weight (e.g. Perrins *et al.* 1973), so the true chick mortality was probably higher than the fledging percentage suggests. These lower weights were partly the result of a lower feeding rate; weight of the chicks' daily ration in 1981 was only 30% of that in 1968–69. It is likely that qualitative, nutritional differences were also important. Harris and

Hislop (1978) found that the clupeids and sandlance which were the preferred foods of puffins at Scottish colonies had a higher calorific value and a higher fat content than the gadids which were only fed to the chicks when these preferred species were scarce. Capelin, like clupeids and sandlance, have a variable but relatively high fat and oil content (Jangaard 1974; see also Table 4), and so they may have been nutritionally superior to the Newfoundland gadids. However, we cannot comment further on this point until the nutritional analyses of the fish brought to the Witless Bay puffin chicks in 1981 have been completed.

Capelin are thus extremely important in the diets of young puffins at colonies in Newfoundland. At first sight it is surprising that their parents could find no substitute prey in 1981, given the variety of foods which puffins are known to bring back to their chicks. Apart from capelin, sandlance, and gadids of several genera, the list at colonies on one or both sides of the Atlantic includes Atlantic herring, Atlantic mackerel (*Scomber scombrus*), sticklebacks (*Gasterosteidae*), gurnards (*Triglidae*), flatfishes (*Pleuronectidae*), gobies (*Gobiidae*), squid, polychaetes, and crustaceans, all of which occur in the northwest Atlantic, as well as such fish as sprat and weevers (*Trachinus vipera*) which do not (Belopol'skii 1957, Myrberget 1962, Corkhill 1973, Ashcroft 1976, Harris and Hislop 1978, Hudson 1979, Lid 1981; see also Table 3, and Leim and Scott 1966). However this gives the misleading impression that the puffin is a versatile bird with a wide choice of potential preys. In actual practice, the birds are limited to prey with an average body depth of 15 mm (maximum 26 mm; Swennen and Duiven 1977); to species with a relatively high calorific value and fat content (Harris and Hislop 1978); and, for maximum foraging efficiency (see above), to species which school. This means that there are only four prime species in the Witless Bay area: capelin, sandlance, and young Atlantic herring and Atlantic mackerel (Leim and Scott 1966). It is not clear why the puffins did not, or could not, increase their consumption of sandlance to compensate for the scarcity of capelin in 1981. It is possible that the bulk of the sandlance population is in the relatively shallow waters of the Grand Banks (e.g. Winters 1983), *ca.* 85 km from the colony at their nearest point, and thus probably outside the birds' foraging range (see above). Eastern Newfoundland is at the northern edge of the range of mackerel in Canadian waters and the species' main spawning grounds are in the Gulf of St. Lawrence (Leim and Scott 1966); the puffins almost certainly could not have had access to the young fish, small enough for them to take. There is an important spawning ground for herring off the south coast of Newfoundland (Leim and Scott 1966). However, the prevailing currents would tend to carry the larvae westwards towards the Gulf of St. Lawrence where, like the mackerel, the young fish would be beyond the birds' foraging range. In short, there seems to be no acceptable substitute for capelin available to the puffins which breed in southeast Newfoundland.

The situation in Witless Bay in 1981 has close parallels with recent events at Røst in the Lofoten Islands, northern Norway, where the puffin colony of *ca.* 700 000 pairs is the largest in Norway (Brun 1979). The preferred prey at this colony was formerly young Atlantic herring, but these have been virtually absent since 1969 (Anon. 1972–79) and, as at Great Island, the adult birds have been bringing young gadids to their chicks instead (Lid 1981, see also Mills 1981). With the exception of 1974, when sandlance and young Atlantic mackerel were available, virtually no young puffins have fledged from this colony since 1969; most die of starvation within the first 10 days after hatching (Lid 1981). Common Murres, Razorbills, and Kittiwakes breeding in the Røst area have also had a very low breeding success (Barrett 1981). The Norwegian fisheries statistics (Anon. 1972–79) suggest that Røst is too far away for the birds to turn to alternative prey, such as capelin farther east off Finnmark, or sprat farther south, off southwest Norway. By contrast the seabird colonies in Finnmark and southwest Norway are apparently breeding successfully (Barret 1981).

Seabirds elsewhere have had varying success in adjusting to the scarcity of a preferred prey species. Harris and Hislop (1978) show that puffins at Scottish colonies have access to several alternative preys — sprat, sandlance, and young herring as well as young gadids — and these act as "buffers" which allow the birds to respond to temporary shortages with reduced breeding success at worst, rather than outright failure. In British Columbia the Rhinoceros Auklet (*Cerorhinca monocerata*), a small Pacific auk, was able to adjust to a scarcity of sandlance by taking sauries (*Cololabris saira*) instead, although the size and nutritional qualities of this alternative were not completely satisfactory and many young auklets starved (Vermeer 1978, 1980; Vermeer *et al.* 1979). However, the Common Murres and Tufted Puffins (*Lunda cirrhata*) breeding in the same area could not make this adjustment apparently because they, unlike the auklets, were unable to feed at night when the sauries were available close to the surface. The principal food of the three guano birds of the Peruvian upwelling system, the Piquero Booby (*Sula variegata*), pelican (*Pelecanus thagus*), and Guanay Cormorant (*Phalacrocorax bouganvillei*), is normally the superabundant anchoveta (Murphy 1936, Jordán 1967). From time to time an intrusion of warm tropical water (the "El Niño" phenomenon) suppresses the upwelling; the fish become very scarce and the guano-bird populations decline drastically (Murphy 1936, Továr and Galarzo 1977, Valdivia 1978). The other preys available to the birds, such as sardines (*Sardinops sagax*) and pejerreyes (*Odontesthes regia*) (Továr and Fuentes 1980), are evidently quantitatively or qualitatively inadequate to support them. In the analogous Benguela upwelling the South African anchovy has recently increased relative to the formerly dominant pilchard and other species. The populations of the South African guano birds, the Cape Gannet (*Sula capensis*), Cape Cormorant (*Phalacrocorax capensis*), and Jackass Penguin (*Spheniscus demersus*) have all declined as a consequence of this. The penguin is the species most affected because its limited foraging range apparently restricts its ability to adjust to the different and less predictable migrations of the anchovies, in contrast to those of the pilchards, its preferred prey (Crawford and Shelton 1978, Crawford 1981). These examples suggest that the more specialized seabird species have fewer choices of prey than might at first appear, and that the scarcity or absence of a preferred species is usually detrimental to them.

Other species of seabirds have adapted more successfully to changes in their food supply, but these are generalist feeders and the changes have usually taken the form of the exploitation of human wastes: for example, the Northern Fulmar in the boreal North Atlantic (Fisher 1952), the Black-legged Kittiwake in Norway and elsewhere (e.g. Norderhaug *et al.* 1977), and the Herring and Great Black-backed gulls in eastern North America (Drury 1973–4). However, the breeding success and, ultimately, the sizes of the populations of specialist fish-feeders like the

alcids and the guano birds almost always decline when preferred items in their diet become unavailable and there is no acceptable alternative. In general, the decline is sharpest in the species or the colonies which rely on the fewest species of prey.

7. Seabirds and the Newfoundland capelin fishery

In the examples quoted above, the fluctuations in the availability of prey at the Scottish and British Columbian alcid colonies were apparently the result of natural phenomena (Harris and Hislop 1978; Vermeer 1978, 1980; Vermeer *et al.* 1979). On the other hand, the scarcity or absence of the birds' preferred prey in other cases was the direct or indirect result of fisheries. This is true of the decline of pilchards off South Africa (Crawford and Shelton 1978, Crawford 1981) and of Atlantic herring off Norway (Anon. 1972–79). The collapse of the anchoveta population off Peru was initiated by an "El Niño" event, but compounded by overfishing of the surviving stock (Valdivia 1978).

The fishery for capelin off Newfoundland has expanded dramatically in the last 10 years. To what extent could this have contributed to the scarcity of these fish off Witless Bay in 1981?

Capelin are or have been harvested for food, fishmeal, fertilizer, and bait (Jangaard 1974). The traditional fishery in Newfoundland took capelin close to the spawning beaches and accounted for *ca.* 23 000 t/year around 1900, declining to *ca.* 5000 t by the late 1970s (ICNAF/NAFO 1963–82; Templeman 1948; see also Fig. 2). Meanwhile a large offshore fishery developed in the Barents Sea in the early 1960s, and was extended to Icelandic waters soon afterwards (ICES 1963–82, Jangaard 1974). It extended farther west to the Grand Banks in the early 1970s, and the catch reached a peak of *ca.* 350 000 t/year by mid-decade (ICNAF/NAFO 1963–82; see also Fig. 2). In the spring of 1978 the rate of recruitment of young capelin into the stocks was found to be very low, and the offshore fishery was suspended and remains so, apart from a limited harvest in subarea 2J (Carscadden *et al.* 1982; Carscadden, this volume). At just that time, however, the inshore fishery expanded rapidly to supply the Japanese market with the roes of mature female capelin (Anon. 1982, Rowe and Collins 1982). Most of this harvest is taken in subarea 3L (stock B), especially in Trinity and Conception bays (Figs. 1 and 2). Landings of 24 529 t were reported from this subarea in 1981 though the actual catch was probably at least twice this figure, because of the inevitable wastage of males and unripe and substandard females which accompany a specialized fishery of this kind.

There is a parallel between the expansion of the capelin fishery off eastern Newfoundland and the decline of the breeding success of the puffins at Witless Bay. Capelin were abundant in the Witless Bay area in the late 1960s, just before the start of the offshore fishery in subarea 3L, but scarce in 1981 after a decade of inshore and offshore fishery there for stock B (Table 3). Is there a causal connection? Capelin mature and spawn at 3–5 years of age (Carscadden, this volume). This interval is too long for the scarcity of 1981 to have been caused by overfishing the spawning stock inshore, because the inshore fishery did not start to expand until 1979. It could, however, have been the result of overfishing *offshore*, in 1976 and 1977, just before that fishery was suspended. There is evidence that offshore capelin were overfished in the 1970s (Carscadden, this volume), but the population affected was stock C, which spawns on the Southeast Shoal out of range of the Witless Bay seabird colonies, and not stock B in subarea 3L. Carscadden points out that the fishery at its peak was taking only *ca.* 10% of the exploitable biomass (e.g. Table 5), seemingly too small a proportion to affect the population as a whole. He suggests that the decline in the recruitment rate which was detected on the Grand Banks in spring 1978 reflects the dying-out of the unusually large year-class of capelin that was spawned in 1973. He notes that the size of a year-class depends on many factors among which the unpredictable effects of the weather on egg and larval survival are particularly important (e.g. Frank and Leggett 1981*a*, 1981*b*), and that it is not necessarily related to the size of the spawning population. Moreover, there is not necessarily a correlation between the biomasses of the capelin and its predators, as Akenhead *et al.* (1982) note for Atlantic cod. It is also possible that capelin were present and abundant off Witless Bay in 1981 but, because of high surface temperatures, were spawning in deep water instead of on the beaches (e.g. Templeman 1948). This might have placed them below the puffins' diving limits (see above). The failure of the Witless Bay puffins to find capelin in 1981 may therefore have been the result of a scarcity of fish brought about either by naturally occurring factors, by the fishery, or by a change in the behaviour of the spawning fish, or by a combination of all of these. It is therefore not possible to go further on the present evidence.

8. Discussion

Capelin are extremely important to many predators in eastern Newfoundland waters; this is especially true of the seabirds. It is clear that the more specialized species, such as murres and puffins, have few acceptable alternative prey available to them when capelin are scarce off Newfoundland. The reproductive strategy of such birds is to maintain a stable population by balancing a low natural adult mortality rate against a low annual reproductive rate combined with a long period of pre-breeding adolescence (e.g. Ashmole 1971, see also Table 1). Up to a point, the populations can remain stable in the face of irregular, natural environmental perturbations which temporarily increase adult mortality or reduce reproductive success; the response of Scottish puffins to natural fluctuations in the abundance of their various prey species (Harris and Hislop 1978) is a case in point. However, such a strategy makes them especially vulnerable to additional, *repeated* mortalities directly or indirectly imposed on them, in Newfoundland and elsewhere, by such human activities as excessive hunting, drownings in gill nets, oil pollution, and competition from the fisheries. The almost complete breeding failure of the puffins on Røst since 1969 (Lid 1981), apparently due to the overfishing of their preferred prey, will inevitably result in a massive decline in the population as the older birds die off, and the species' low reproductive rate will make the population slow to recover if and when the herring stock recovers. It is important to keep a close watch on the comparable recent events in the puffin population at Witless Bay to determine the extent to which these puffins are also being affected by fluctuations in their principal prey, capelin. Such monitoring will provide us with advance warning of the state of the puffin population and, by extension, of the capelin stocks as well.

For this, we need more information about the feeding ecology of seabirds in general, at Witless Bay and elsewhere. We also need to know much more about the population biology of capelin. It is unfortunate that the capelin fishery has expanded faster than its scientific base, and that most current research on the species is devoted to stock assessment techniques and other aspects of management, rather than basic biology (Carscadden, this volume). Even here, there is still no reliable method of assessing the *absolute* as opposed to the relative biomasses of capelin stocks. This makes it almost impossible to judge how realistic are the quotas set for the capelin fishery, not just in relation to the capelin population as a whole, but also to the requirements of the populations of the various animals which prey on these fish. To allow for these unknown factors the catch limits are purposely set at conservative levels: 10% of the projected capelin "surplus," or 30 000 t, in subarea 3L in 1981 (NAFO 1981). But are they conservative enough? Even if we ignore the importance of *local* as opposed to overall capelin abundance, and the inaccessibility of the deep schools to most seabirds, the evidence suggests that they are not. The overall biomass estimates, for all their limitations, seem to show a decline of the order of 75–90% in capelin biomass off eastern Newfoundland during the 1970s, perhaps to a level below that needed to support the predators' populations at the levels they held only 20 years ago (see above, and Table 5). If this is true, the predators of the capelin can respond only by switching to an alternative prey — an unlikely option for seabirds, at least — or by reducing their own biomass by emigration or starvation. In the latter case we have too few data to predict whether the decline in the populations of the higher predators will be total or only partial, and there is a danger that the answers will not become apparent until it is too late for remedial measures. This is an unsatisfactory situation from every point of view.

In conclusion, we are struck by the extreme vulnerability of ecosystems which depend on a single central prey species, however abundant that species may appear to be. We find it very disturbing that human exploitation should already have reached a high level without any proper means of understanding, or even measuring, its effects on the populations of such species, let alone on those of the predators which depend on such prey.

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Net-mortality of Common Murres and Atlantic Puffins in Newfoundland, 1951–81

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1. Abstract

Band recoveries (N = 315) over 26 years (1951–77) and three surveys of seabird bycatch in inshore fishing nets (1972, 1980–81) indicate that there has been a substantial net-mortality of Atlantic Puffins (*Fratercula arctica*) and Common Murres (*Uria aalge*) in Newfoundland coastal waters for the past 2 decades. Offshore (e.g. Grand Banks) gill-netting is limited, but some data suggest that murre net-mortality also occurs offshore at murre wintering areas. The vast majority of inshore net-mortality incidents occur over a 2-week period during the annual inshore spawning migration of capelin (*Mallotus villosus*), the major prey item for alcids in eastern Canada. Most murres (83%) were drowned in bottom-set (30–185 m) cod (*Gadus morhua*) gill nets, whereas more puffins were drowned in surface-set salmon (*Salmo salar*) gill nets or cod traps (55%) than in cod gill nets (45%). Murre band recoveries, colony censuses, and fishing-effort data suggest that at the second largest Common Murre colony in Newfoundland (Witless Bay Seabird Sanctuary, 77 000 breeding pairs) net-mortality was relatively low in the 1950s and early 1960s, but increased during the 1960s as the murre population grew in size and gill-net fishing effort increased in the colony area. By 1971, net-mortality accounted for 70% of murre band recoveries and calculations show that almost 30 000 breeding adults, or about 20% of the local breeding population, were drowned in that year. More reliable estimates of alcid bycatch in the Witless Bay area have been made on the basis of actual bycatch surveys. In 1972 about 20 000 adult murres, or 13% of the breeding stock, were killed in gill-nets. Net-mortality of murres apparently diminished through the 1970s as capelin stocks declined and fewer birds foraged in heavily netted inshore areas. Bycatch surveys in the Witless Bay area in 1980–81 revealed that, relative to previous years, murre net-mortality was greatly reduced and resulted in the loss of only 3–4% of the breeding stock. Even these low mortality rates, however, are cause for concern as adult murre mortality from all sources (including hunting, oil, and natural mortality) should not exceed 6–12% per annum to maintain a stable breeding population. Little is known about the magnitude of net-mortality at other major Newfoundland murre colonies though it is known to be a problem in all colony areas. The bycatch of adult Atlantic Puffins in the Witless Bay area was low compared to murre bycatch and in 3 years of study never exceeded 1.6% of the breeding population. During the 1970s, fishing effort increased five-fold in colony areas and we predict that if capelin spawning stocks return to early 1970s size, then net-mortality of puffins and murres in Newfoundland coastal regions will increase dramatically. Indeed, preliminary examination of 1982 capelin spawning and seabird bycatch data suggests that capelin were much more abundant inshore and murre bycatch increased two- to three-fold over 1981.

2. Résumé

La récupération de bagues (N = 315) pendant 26 années (1951 à 1977) et trois relevés d'oiseaux emprisonnés dans les filets de pêche côtière (1972, 1980–1981) révèlent que la mortalité des Macareux arctiques (*Fratercula arctica*) et des Marmettes communes (*Uria aalge*) dans les filets de pêche côtière a été forte dans les eaux de Terre-Neuve durant ces 20 dernières années. La pêche hauturière aux filets maillants (par exemple à Grand Banks) est limitée, mais certaines données laissent croire que les marmettes se noient également dans les filets en haute mer dans leurs zones d'hivernage. La plupart des décès dans les filets de pêche côtière surviennent dans une période de deux semaines durant la migration annuelle, vers les frayères du capelin (*Mallotus villosus*), principale proie des alcidés de l'est du Canada. La plupart des marmettes (83 %) se sont noyées dans des filets maillants de fond (30 à 185 m) de la pêche à la morue (*Gadus morhua*) tandis que plus de macareux se sont noyés dans des filets maillants de surface de la pêche au saumon (*Salmo salar*) ou dans des trappes à morue (55 %) que dans des filets à morue (45 %). Les données sur les bagues récupérées, les recensements de colonies et l'effort de pêche indiquent que dans la deuxième colonie en importance à Terre-Neuve (Sanctuaire d'oiseaux aquatiques de Witless Bay, 77 000 couples de nicheurs), la mortalité des Marmettes communes dans les filets de pêche a été relativement faible durant les années 1950 et au début des années 1960, mais a augmenté durant la décennie 1960 avec l'accroissement de la taille de la population et de l'effort de pêche aux filets maillants dans la région abritant la colonie. Vers 1971, 70 % des bagues ont été récupérées sur des marmettes emprisonnées dans les filets, et des calculs montrent que près de 30 000 adultes nicheurs, ou environ 20 % de la population nicheuse locale, se sont noyés cette année-là. Des estimations plus sûres des captures d'alcidés à Witless Bay ont été effectuées à partir des données obtenues réellement dans les relevés d'oiseaux capturés. En 1972, environ 20 000 marmettes adultes, soit 13 % de la population nicheuse, se sont tuées dans des filets maillants. La mortalité de cette espèce dans les filets a diminué apparemment durant les années 1970 avec une baisse des stocks de capelan et du nombre d'oiseaux se nourrissant dans les régions côtières où la pêche au filet est intensive. Des relevés

sur les captures dans la région de Witless Bay en 1980–1981 ont révelé que, par rapport aux années antérieures, la mortalité des marmettes dans les filets avait diminué considérablement et n'avait entraîné qu'une perte de 3 à 4 % de la population de reproducteurs. Toutefois, même ces faibles taux de mortalité suscitent certaines préoccupations, car la mortalité des marmettes adultes, quelle qu'en soit la cause (dont la chasse, les déversements de pétrole et la mortalité naturelle), ne doit pas dépasser 6 à 12 % par année pour que l'effectif de la population de nicheurs demeure stable. On ne possède que peu de données sur l'ampleur de la mortalité dans les filets de pêche dans d'autres importantes colonies de marmettes de Terre-Neuve, bien qu'on présume qu'elle constitue un problème dans toutes les régions abritant des colonies. Le nombre de Macareux arctiques adultes capturés dans la région de Witless Bay a été faible comparativement à celui des marmettes, et durant les trois années de l'étude, il n'a jamais dépassé 1,6 % de la population de reproducteurs. Au cours des années 1970, l'effort de pêche a quintuplé dans les régions abritant des colonies, et les auteurs prévoient que si l'effectif des stocks de capelan géniteur revient aux valeurs du début des années 1970, la mortalité des macareux et des marmettes dans les filets de pêche des régions côtières de Terre-Neuve augmentera de façon radicale. De fait, une étude préalable des données de 1982 sur le frai des capelans et les captures d'oiseaux aquatiques laisse croire que les capelans étaient beaucoup plus abondants dans les zones côtières et que le nombre de marmettes capturées a été de 2 à 3 fois plus élevé en 1981.

3. Introduction

Little research has been conducted on seabird mortality associated with commercial fishing operations. Seabirds are known to be drowned in fishing nets in the northeast Atlantic (Holgerson 1961, Bourne 1971, Brun 1979), off Greenland (Tull *et al.* 1972, Christensen and Lear 1977, Evans and Waterston 1976), and in the Pacific (Ogi and Tsujita 1973, DeGange 1978, King *et al.* 1979, Ainley *et al.* 1981), but to date, little is known of the problem in Newfoundland waters where a substantial salmon and cod gill-net fishery coexists with large seabird populations.

The most comprehensive data on net bycatch have been obtained from research on the west Greenland salmon (*Salmo salar*) drift-net fishery. Tull *et al.* (1972) estimated an average Thick-billed Murre (*Uria lomvia*) bycatch of 500 000 ± 50% birds per year for the years 1969–71 by extrapolating from an observed ratio of murres to salmon in research vessel drift nets to the total west Greenland drift-net salmon catch.

Christensen and Lear (1977) re-examined seabird bycatch in the Greenland fishery during the course of joint International Council for the Exploration of the Seas – Internation Commission on North Atlantic Fisheries (ICES/ICNAF) salmon-tagging experiments in 1972. They found the relationship between seabird bycatch and salmon catch to be weak and consequently derived their estimates of seabird mortality solely on a catch-per-unit-effort basis. They estimated that in 1972 about 207 000 Thick-billed Murres drowned in drift nets along with 19 other seabird species including 10 000 Dovekies (*Alle alle*), 2000 Black Guillemots (*Cepphus grylle*), and 2000 Greater Shearwaters (*Puffinus gravis*). In addition, they concluded that the probability of seabird net-entrapment depends on many factors associated with the birds themselves, particularly their activity pattern, size, shape, and feeding behaviour, and that the relative abundance of a seabird species in bycatch did not necessarily reflect its abundance at sea. Also, the most accurate measure of fishing effort with which seabird mortality could be correlated was the product of the quantity of nets (total length in kilometres) multiplied by fishing time (in hours), or kilometre-hours of effort. This approach has some drawbacks, however, as it does not take into account the variable effects of wind, tide, currents, and sea-surface conditions, or prey fish species abundance and distribution, on seabird net-entrapment.

More recently, Ainley *et al.* (1981) found that for some seabird species (e.g. Thick-billed Murre and Short-tailed Shearwater (*Puffinus tenuirostris*)), there was a positive correlation between abundance at sea and net entrapment in high seas salmon gill nets in the North Pacific Ocean and Bering Sea. The highest densities and catch rates of seabirds occurred within 100 km of the Aleutian Islands and in the productive waters of the Alaskan Stream and Bering Current. The most commonly caught species were those that fed beneath the ocean surface by diving or pursuit plunging. They estimated that 266 500 birds were killed annually in the offshore Japanese salmon gill-net fishery between 1952 and 1979 and, of particular relevance to the Newfoundland situation, they demonstrated that bird catch rates increased logarithmically as distance to major seabird colonies decreased.

Newfoundland alcids, especially the Common Murre (*Uria aalge*) and Atlantic Puffin (*Fratercula arctica*) are predominantly capelin (*Mallotus villosus*) predators (Tuck 1961, Nettleship 1972). In summer, an estimated one million Common Murres and 500 000 Atlantic Puffins breed in Newfoundland (Nettleship 1980) and forage for capelin in coastal waters also intensively fished by people (Nettleship 1977). Until recently little has been known of the impact of the Newfoundland inshore fishery on seabirds. King *et al.* (1979) stated:

> There are as yet no estimates of the total alcid mortality from this fishery, although the annual catch of birds is believed to be smaller during the present (1970s) than during the last decade (1960s) because the fishing effort is reduced and fishermen in the area now avoid setting nets near alcid concentrations because of the annoyance of having to remove birds from their nets.

In this paper, we will present evidence that there were and still are large numbers of alcids being killed in the inshore fishery. Many alcids are drowned in fish nets set close to their breeding colonies as well as many kilometres away. Although alcid bycatch has diminished in recent years, this is not due to a decreased fishing effort: the inshore fishery has increased five-fold between 1973 and 1980 (as judged by the number of person-hours fished and the number of gill nets in use). Instead, it is related to changes in capelin biomass and interyear differences in inshore spawning by capelin.

The offshore gill-net fishery in Newfoundland may also result in significant alcid mortality. In addition to resident alcid populations, an estimated four million Thick-billed Murres from the eastern Canadian Arctic and several million Dovekies from Greenland arrive in autumn to spend the winter foraging along the east coast of Newfoundland and on the Grand Banks (Brown *et al.* 1975, Gaston 1980). Although the offshore cod gill-net fishery in Newfoundland

is relatively small (about 6000–9000 nets in use between May and December, D. Kulka, pers. comm., Department of Fisheries and Oceans [DFO], Enforcement Branch, St. John's), it is concentrated in areas known to be important to wintering populations of alcids (Brown *et al.* 1975). Preliminary data from DFO salmon-tagging experiments in 1979 and 1980 (D. Reddin, unpubl. data) indicate that alcid bycatch is associated with gill-netting operations in these areas.

The purpose of this paper is to review the available data on net-mortality of alcids breeding at major colonies in Newfoundland, attempt a preliminary assessment of its importance as one of several mortality factors affecting alcid populations, examine its possible relationship to capelin abundance, predict future trends, and reveal what research is required in the future.

4. Capelin

Prior to 1966, capelin research centred on life history, distribution, and racial studies (Templeman 1948, Pitt 1958, Winters 1966). Consequently, little is known about capelin abundance before this time, although reports of unusually low inshore capelin spawning efforts do not appear in the literature. Between 1950 and 1971 anywhere from 3000 to 20 000 t of capelin were harvested annually by inshore fishermen for use as fertilizer and bait (Campbell and Winters 1973). In anticipation of future large-scale exploitation, an assessment of capelin abundance was initiated in the mid 1960s (Templeman 1967) and an offshore fishery was opened in 1972 (Pinhorn 1976) with landings for that year totalling 70 800 t. These offshore landings rose to 360 500 t in 1976 and declined to only 11 000 t in 1979 (Akenhead *et al.* 1981). Estimates of total capelin biomass in the Newfoundland region are available (Carscadden and Winters 1980) for 1972–79 and show a peak of capelin biomass in 1975 and 1976 of about 1.3 million metric tons for both years and a decline to 350 000 t in 1979.

In summary, in the late 1960s and early 1970s capelin were abundant throughout their range in Newfoundland and southern Labrador (Jangaard 1974), but in recent years (1977–81) there has been a marked decline (five- to ten-fold) in capelin numbers both off shore (Carscadden and Miller 1980, 1981; Carscadden *et al.* 1981; Miller and Carscadden 1981; Carscadden, this volume) and inshore (J. Carscadden, pers. comm.). Although historical information on inshore spawning effort is largely qualitative, it is correlated with the size of offshore stocks because it is the mature fish from offshore stocks that move inshore to spawn (Jangaard 1974). (For a more complete analysis of historical capelin population trends, see Carscadden, this volume.)

5. Inshore net-mortality

5.1. Introduction

From all data collected, it is evident that most inshore alcid net-mortality coincides with the presence of capelin in fishing areas. Given the historical trends in capelin abundance and the correlation between alcid net-mortality and capelin presence, one can assess the relative significance of the inshore alcid net-mortality estimates given in Table 1 from band recoveries of Common Murres between 1951 and 1977 (Canadian Wildlife Service [CWS] files) and surveys of net-mortality made in 1972 (D.N. Nettleship), 1980, and 1981 (J. Piatt) in the Witless Bay Seabird Sanctuary area (Fig. 1*b*). Details of these data sets now follow with explanations of (1) how the net-mortality estimates were derived, and (2) what these results suggest considering the timing and distribution of net-mortality and the types of fishing gear involved.

5.2. Magnitude of net-mortality based on recoveries of banded Common Murres

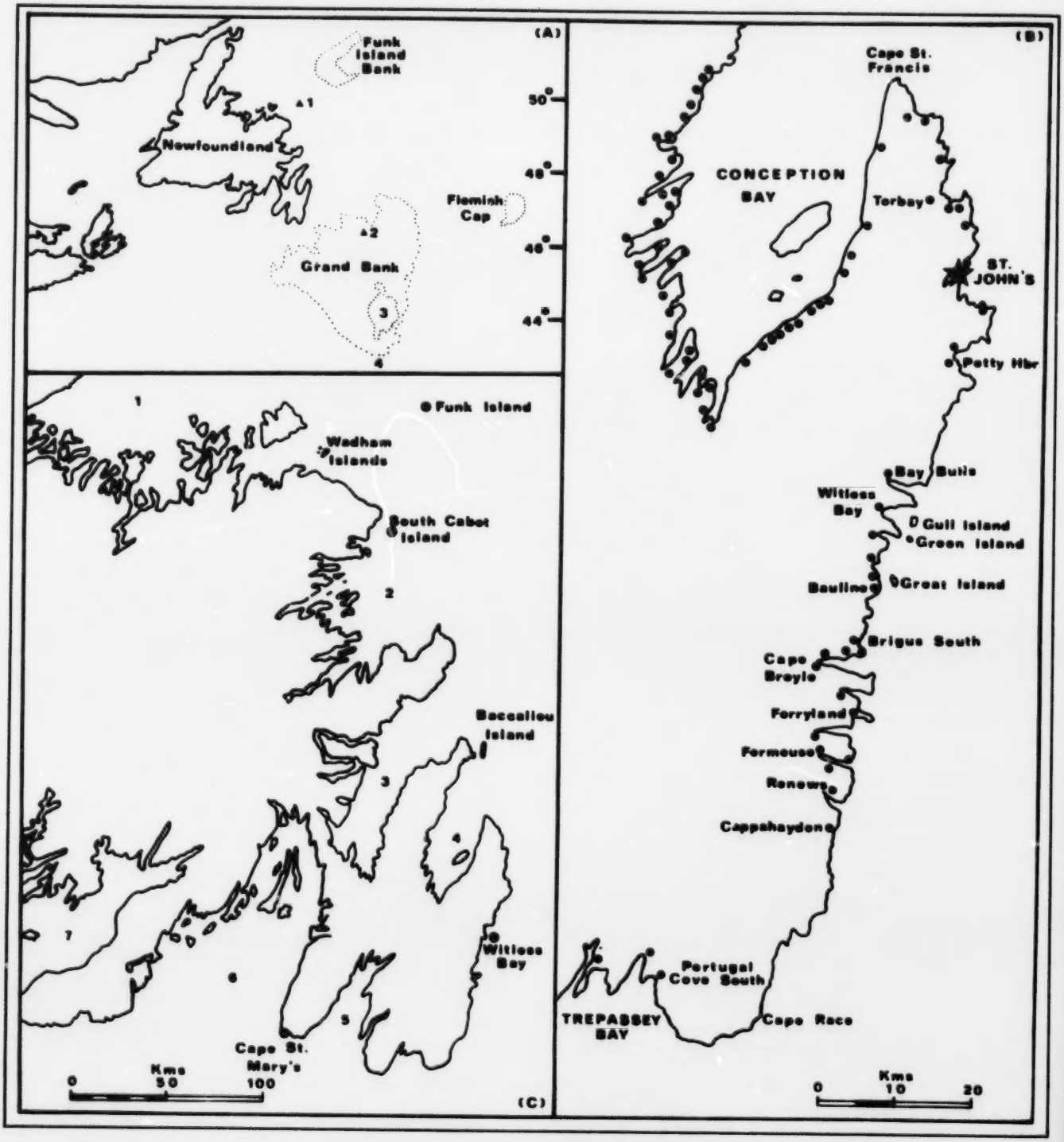
Common Murre chicks (N = 9740) on Green Island, Witless Bay (Fig. 1*b*) were banded by L.M. Tuck and co-workers of the CWS during 1951–56 and 1966–70 and band recoveries were made during 1951–62 and 1966–77 (CWS files). Over 90% of all band recoveries from the 1950s and 1960s banding efforts were made between 1953 and

Table 1
Inshore net-mortality of Common Murres and Atlantic Puffins in the Witless Bay Seabird Sanctuary area, 1954–81

Time period	Study method	Assessment of mortality	Est. no. of birds killed		% breeding population killed	
			Common Murre	Atlantic Puffin	Common Murre	Atlantic Puffin
1954–56	Band-recovery analysis: Common Murre*	Population size × % mortality (3-year average)	7800 ± 4900	—	6.2	—
1967–71	Band-recovery analysis: Common Murre*	Population size × % mortality (5-year average)	27 200 ± 9700	—	14	—
1970	Band-recovery analysis: Common Murre*	Population size × % mortality	35 600	—	18	—
1971	Band-recovery analysis: Common Murre*	Population size × % mortality	38 000	—	20	—
1972	Daily record of net-mortality through fishing season by one fishing crew†	No. birds drowned/net/season × total no. nets in foraging area	25 200	2400	13	0.59
1980	Daily record of net-mortality by 8 fishermen and 5 qualitative reports‡	No. birds drowned/net/season × total no. nets in fishing area, summed for 5 communities	4200	7900	2.7	1.6
1981	Daily record of net-mortality by 20 fishermen and 71 qualitative reports‡	No. birds drowned/net/season × total no. nets in fishing area, summed for 15 communities	6260–8100	1210–2104	3.3–4.2	0.25–0.43

*Data from CWS files and Threlfall and Tuck (in prep.).
†Data from D.N. Nettleship (unpubl.).
‡Data from J. Piatt (unpubl.).

Figure 1
(*a*) Offshore areas where alcid mortality in nets is known to occur: 1, Funk Island; 2, Virgin Rocks; 3, Southeast Shoal; and 4, Tail of the Banks. (*b*) Southeastern inshore area showing the distribution of fishing communities around the Witless Bay Seabird Sanctuary (Gull, Green, and Great islands). (*c*) Other inshore fishing areas where alcid net-mortality occurs are as follows: 1, Notre Dame Bay; 2, Bonavista Bay; 3, Trinity Bay; 4, Conception Bay; 5, St. Mary's Bay; 6, Placentia Bay; and 7, Fortune Bay. Also shown are the six seabird colonies in Newfoundland (names given)



1958 and 1967 and 1972, respectively. Due to band loss (Tuck 1961), few recoveries were made later than 3 years after banding effort had ceased.

Analysis of murre band recoveries (Table 2) clearly shows the magnitude of net-mortality for Green Island murres. Ninety-three of 315 murres (30%) recovered over 26 years were found in fishing nets. This is a very high proportion compared to murre recoveries in Britain where only 3.8% of all British murre recoveries ($N = 552$) up to 1972 were from "fishing tackle" (Birkhead 1974). In addition, many murres in the "found dead" category may have been discarded after removal from nets (Tuck 1961), which raises the net-kill to possibly 40%. No murres banded as adults ($N = 453$) were ever recovered in nets and of all the immature murres recovered from nets ($N = 93$) about 25, 50, and 25% were 1–2, 2–3, and 3–4 year-class birds, respectively.

Separation of these data into the appropriate recovery periods (1951–1962 and 1966–1977), however, better illustrates the more recent situation. The Witless Bay murre population has increased from roughly 20 000 pairs in 1953 (Tuck 1961) to 77 000 pairs in 1972 (Brown *et al.* 1975), while fishing effort has increased markedly (since the 1950s) along with an increase in the use of cod and salmon gill nets (D. Wells, pers. comm., Department of Fisheries and Oceans [DFO], Econ. Br., St. John's). Accordingly, there was an increase in the proportion of net-related mortality from 6% in the 1950s to 49% in the 1960s and early 1970s. If the "found dead" murres are added to this, the proportions become 16 and 60%, respectively. Fish-net recoveries peaked in 1970 and 1971, with 66 and 70% of all recovered murres drowned in fish nets, respectively.

Using these band-recovery figures we calculated the actual number of murres drowned in nets in 1971 in the following manner. Assuming that in each of the years 1966–1971 there were 77 000 breeding pairs of Common Murres at the Witless Bay Seabird Sanctuary (Gull, Green, and Great islands, Brown *et al.* 1975) and that productivity was 0.70 chicks/pair (Birkhead and Hudson 1977, Mahoney 1979), then in each given year 53 900 chicks were fledged. Although Newfoundland band recoveries have yet to be analysed for the construction of life tables, the mortality of murre chicks (0–1 year-class) to first year (1–2 year-class) is considered to be high (Birkhead 1974, Mead 1974) and for the purpose of these calculations at least 50%. Since no 0–1 year-class murres were recovered in nets and few murre fledglings returned in the next year to their natal colonies (Birkhead and Hudson 1977), we attributed none of this first-year mortality ($0.5 \times 53\,900 = 26\,950$ murres) to drowning in nets. If we consider that 4–5 year-class murres are breeders and that survival to this age class is about 30% (Birkhead and Hudson 1977), then about 16 200 chicks ($0.3 \times 53\,900$) produced in any given year would have survived to breeding age. Thus, the number of immature murres (1–2, 2–3, and 3–4 year-classes) dying between their second and fifth years of life would be approximately 10 800 (27 000–16 200). In 1971, 70% of this mortality was due to drowning in nets, which means about 7600 immature murres drowned. From recent bycatch surveys (section 5.6), however, it appears that the ratio of immature to adult murres caught in nets is about 1:5 respectively. Thus, the total number of murres killed in nets at Witless Bay in 1971 may have equalled 38 000.

Similar calculations were made for each year in which more than 15 murre band recoveries were made (Table 1). In 1970, about 35 600 murres may have drowned in nets. For the years 1967–1971 inclusive, the calculated number of murres killed in nets was 27 200 ± 9700. Again, for 1954–56 (and assuming a murre population of 50 000 pairs: Tuck 1961), 7800 ± 4900 murres were killed in fishing nets.

Table 2
Comparison of recoveries of Common Murres banded on Green Island, Witless Bay, for different time periods

Time period	Total no. of banded birds recovered	Cause of death: Drowned in fishing gear No.	%	"Found dead" No.	%	Other No.	%
1951–77	315	93	30	32	10	193	60
1951–62	144	9	6	14	10	121	84
1966–77	171	84	49	18	11	72	40
1970	29	19	66	1	3	9	31
1971	33	23	70	0	0	10	30

There is little doubt that these estimates of murre bycatch are excessive because the return of bands from birds recovered in fishing gear is likely to be proportionately higher than band recoveries from birds killed in other ways (e.g. oil, hunting, or natural mortality, Mead 1974). Nonetheless, compared to the estimates in sections 5.4–5.6 and Table 1, these figures appear to be of the right order of magnitude and provide a relative assessment of murre net-mortality in Newfoundland from 1954 to 1971. Based on these figures it appears that murre net-mortality was low in the 1950s and early 1960s resulting in an annual adult mortality equivalent to about 6% of the breeding population (number of murres killed × proportion of adults − total number of individuals breeding, i.e. $7800 \times 0.8 \div 100\,000$). Net mortality increased in the late 1960s and adult mortality averaged about 14% of the breeding population during 1967–71 inclusive. In 1970 and 1971, the calculated adult mortality peaked at about 18 and 20% of the breeding population, respectively. Insufficient band recoveries were made during 1972–77 to assess net-mortality, but more reliable surveys of actual bycatch (sections 5.4–5.6) and trends in capelin abundance indicate that net-mortality declined through the 1970s.

5.3. Net-mortality of banded Common Murres: type of fishing gear, timing, and distribution

In Newfoundland, Common Murres are concentrated at their colonies from April to July and most are found offshore by August (Tuck 1961, Mahoney 1979). Thus murres are abundant in the periphery of their colonies during the time of major inshore fishing effort (LeMessurier 1980) for herring (*Clupea harengus*) in April, salmon in mid May to July, and cod in early June to October.

In addition to the Green Island band returns, there are data on net-recoveries of Common Murres ($N = 21$) which were banded as chicks on Funk Island. Together, these recoveries ($N = 114$) indicate the types of fishing gear responsible for murre net-mortality (Table 3). The ratio of murres killed in cod gill nets to salmon gill nets is about 2:1 and 89.5% of all recoveries were made from gill nets. The remaining 10.5% of recoveries were evenly distributed between cod traps, trawl lines, and herring nets.

The majority of band recoveries ($N = 114$) occurred in the months of May (12%), June (50%), and July (24%) with the remaining 14% spread evenly over the other 9 months of the year. The 86% of recoveries in May–June correspond to the known pattern of inshore capelin spawning in Newfoundland which typically peaks in June (Jangaard 1974). The 14% of recoveries outside this period may provide a biased estimate of non-capelin associated mortality since banded murres would less likely be noticed during the times when large numbers were being removed from nets (May–July) than at other times of the year when murre bycatch was unusual (August–April).

Only 12 (11%) of the recoveries were made outside a 70 km radius (estimated foraging range) of a major seabird colony (Fig. 1*c*) and half of these ($N = 6$) were also outside the May–July period. Most of these strays ($N = 9$) were caught in fishing gear on the southwest coast of Newfoundland and in Placentia Bay.

5.4. Net bycatch survey, 1972

In 1972, a fisherman in Bauline East, 2 km from Great Island (Fig. 1*b*), recorded the number of birds caught in his fishing gear (Table 4) throughout the fishing season (16 May – 2 November). A kill of 561 birds was recorded (502 Common Murres, 12 Thick-billed Murres, 46 Atlantic Puffins, and 1 Black Guillemot), with only one bird (Black Guillemot) caught outside the time capelin were judged to be present by the fisherman (17 June – 2 August). Murres were caught ($N = 464$) in cod gill nets (monofilament nylon, 140 mm mesh) and cod traps ($N = 50$), but never in salmon gill nets (nylon, 140 mm mesh) which were in the water from 16 May to 16 June (i.e. before the arrival of capelin in the inshore area). Mortality of Common Murres in gill nets was highest (15.7 birds/net/day, $N = 224$) during the first week of capelin spawning (17–23 June) with reduced numbers of birds (3.6 birds/net/day, $N = 228$) caught in nets during the remaining 40 days of the capelin period. Common Murres were caught four times in cod traps ($N = 30$, 10, 6, 4) and puffins were only caught in gill nets on 2 days ($N = 40$, 6) in July. No birds were killed in nets after 17 July, although cod gill nets and cod traps were in daily use until 10 August and 2 November, respectively.

Based on an average effort of 5.4 nets/day in use during the capelin period, the estimated rate of alcid mortality in 1972 for the Great Island area was 84 murres/net/season and nine puffins/net/season. In 1972 there were probably about 300 gill nets in operation (D. Wells, pers. comm., DFO, Econ. Br., St. John's) within the area used for feeding by alcids breeding at the Witless Bay Seabird Sanctuary. If we assume that the kill at each net was equal, then the total number of murres and puffins drowned in 1972 may have been as high as 25 200 and 2700, respectively. As before (section 5.2), we calculate that this represents an adult murre and puffin mortality of 13 and 0.6%, respectively, of the local alcid breeding populations. Note that this estimate of murre net-mortality (13% of breeders) is very close to the average murre net-mortality calculated from murre band recoveries for 1967–71 inclusive (14% of breeders, section 5.2). This method of extrapolation, however, may be subject to considerable error. Bycatch surveys in 1980–81 (sections 5.5 and 5.6) indicate that bycatch rates can vary markedly between fishing areas (Tables 4 and 5) and it is impossible to speculate on whether the 1972 bycatch rate observed was typical, low, or high. We can, however, compare maximum murre bycatch rates between years. The maximum observed cod gill-net bycatch rates in 1980 and 1981 of 10.8 and 19.4 murres/net/season, respectively (for Witless Bay, Tables 4 and 5), are only 13 and 23%, respectively, of the 1972 rate of 84 murres/net/season. Similarly, the 1980 and 1981 total bycatch estimates (Table 1), which are based on much more data, are only 16 and 25–32%, respectively, of the 1972 total bycatch estimate. Thus, working back from 1980–81 surveys and

Table 3
Comparison of net-mortality of 114 Common Murres banded as chicks on Green Island or Funk Island, Newfoundland, and recovered between 1951 and 1977, by type of fishing gear

Type of fishing gear	Banded birds, no.	Recovered, %
Gill nets		
Unspecified*	52	46
Salmon	17	15
Cod	33	29
Total	102	89.5
Others		
Cod trap	4	3.5
Trawl-line	4	3.5
Herring net	4	3.5
Total	12	10.5

*Unspecified gill nets were probably all salmon or cod gill nets judging by the date of net-mortality.

Table 4
Summary of alcid bycatch in salmon gill nets and cod gill nets and traps in the Witless Bay Seabird Sanctuary area, 1972 and 1980

				Bird mortality in cod gill nets and traps								Bird mortality in salmon gill nets				Estimated kill for all nets	
						No. birds drowned		± no. birds/net				No. birds drowned		± no. birds/net			
Community	No. fishermen reporting	Minimum distance of nets from nearest colony, km*	Time period kill recorded	Total number of nets	No. nets Sampled	Common Murre	Atlantic Puffin	Common Murre	Atlantic Puffin	Total no. of nets	No. nets sampled	Common Murre	Atlantic Puffin	Common Murre	Atlantic Puffin	Common Murre	Atlantic Puffin
1972																	
Bauline	1	0–2	17 June – 2 August	300	6	502	46	84.0	8.0	?	2	0	0	0	0	25 200	2400
1980																	
Witless Bay	4	0–3	5 July – 16 July	107	65	700 ± 50%	11 ± 25%	10.8	0.17	?	0	—	—	—	—	1156	18
Tors Cove	1	0–3	28 June – 18 July	70	11	88 ± 5%	0	8.0	0	?	0	—	—	—	—	560	0
Bauline	3	0–3	3 July – 10 July	400	47	108 ± 50%	0	2.3	0	?	16	0	350 ± 50%	0	21.8	230	350
Brigus South	1	9–11	24 June – 10 July	0	0	—	—	—	—	44	3	88 ± 5%	57 ± 5%	29.3	19	1289	836
Cape Broyle	4	13–15	25 June – 4 July	23	23	10 ± 5%	0	0.4	0	200	6	28 ± 5%	200 ± 50%	4.7	33.3	950	6660
1980 totals																4185	7864

*Colonies and population sizes (breeding pairs) (from Nettleship 1980):

	Common Murre	Atlantic Puffin
Great Island	2 800	148 000
Green Island	74 000	17 000
Gull Island	680	74 000

considering the high bycatch estimates from murre band recoveries (section 5.2) in 1967–71, we feel that the 1972 bycatch estimate is reasonably accurate.

5.5. Net bycatch survey, 1980

In summer 1980 a survey of alcid bycatch in fishing gear was carried out by collecting information (Table 4) from 13 fishermen actively fishing in inshore waters around the Witless Bay Seabird Sanctuary (Fig. 1*b*). The reliability of data collected has been subjectively estimated and is believed to vary from ± 5% (kill recorded daily by reliable fisherman) to ± 50% (based on personal interviews before and after the season). Alcid bycatch was recorded from 23 June to 19 July in the survey area and because fishermen had most of their gear in operation throughout this period, the total murre and puffin kill was estimated by multiplying the average number of birds killed per net times the total

Table 5a
Fishing effort, sampling effort, and reported alcid bycatch in the Witless Bay Seabird Sanctuary area in 1981

	No. of nets* used			No. of nets sampled			Bird mortality in nets (No. birds drowned)					
							Common Murre			Atlantic Puffin		
Community	CN	SN	CT	CN(†)	SN(†)	CT(†)	CN(†)	SN(†)	CT(†)	CN(†)	SN(†)	CT(†)
Pouch Cove	82	75	20	24	16	11	0	8	0	0	0	0
Flat Rock	42	37	22	16	17	6	0	0	0	0	1	0
Torbay	15	30	20	0	8	5	—	4	0	—	0	0
St. John's	70	24	10	50	20	4	10	4	0	0	0	0
Petty Harbour	0	217	62	0	27(5)	7(1)	—	22(10)	10(0)	—	5(5)	0(0)
Bay Bulls	167	205	35	167	69	9	517	54	0	20	59	0
Witless Bay	114	24	3	114(102)	24(7)	3(1)	2076(1978)	191(56)	15(0)	174(153)	74(35)	0(0)
Tors Cove	70	10	5	60(35)	4(4)	5(3)	192(185)	25(25)	2(2)	4(2)	7(5)	0(0)
Bauline	64	5	5	64	5	1	190	4	0	29	43	0
Brigus South	30	70	8	10(4)	32(10)	7(2)	4(4)	89(80)	3(3)	7(0)	99(94)	19(19)
Cape Broyle	80	135	37	52(34)	21(10)	18(4)	81(81)	39(15)	15(15)	15(15)	30(23)	21(8)
Calvert	107	75	33	33(20)	20(8)	8(2)	175(175)	190(172)	1(1)	0(0)	21(16)	2(2)
Ferryland	59	28	27	20	19	11	2	0	3	0	1	0
Aquaforte	0	33	17	0	8(4)	5(2)	—	5(5)	0(0)	—	10(10)	0(0)
Fermeuse	310	35	20	310(25)	14(4)	1	132(0)	16(2)	1(0)	0(0)	2(0)	0
Renews	200	25	24	68	10	11	64	2	0	0	0	0
Portugal Cove	150	30	30	30	4	2	0	0	0	0	0	0
Totals	1560	1058	378									
All reports ($N = 91$)				1018	318	114	3443	653	40	243	350	42
Type 1 reports ($N = 20$) only				220	52	15	2423	465	21	177	190	29

*Nets used were cod gill nets (CN), salmon gill nets (SN), and cod traps (CT).
†Numbers in parentheses indicate the values obtained from type 1 reports only (most accurate data; see text for details).

Table 5b
Net bycatch rates and total estimated numbers of alcids killed in nets in the Witless Bay Seabird Sanctuary area in 1981*

	Min. dist. of nets from colonies, km†	No. of birds killed/net‡/season						Estimated kill in nets						Estimated kill for all nets	
		Common Murre			Atlantic Puffin			Common Murre			Atlantic Puffin				
Community		CN(§)	SN(§)	CT(§)	CN(§)	SN(§)	CT(§)	CN(§)	SN(§)	CT(§)	CN(§)	SN(§)	CT(§)	Common Murre	Atlantic Puffin
Pouch Cove	60–80	0	.50	0	0	0	0	0	37	0	0	0	0	37	0
Flat Rock	60–70	0	0	0	0	.06	0	0	0	0	0	2	0	0	2
Torbay	50–60	—	.50	0	—	0	0	—	15	0	—	0	0	15	0
St. John's	30–40	.20	.20	0	0	0	0	14	5	0	0	0	0	19	0
Petty Harbour	25–30	—	.81	0	—	.19	0	—	176	0	—	41	0	176	41
			(2.0)	(0)		(.50)	(0)		(434)	(0)		(109)	(0)	(434)	(109)
Bay Bulls	1.5	3.1	.78	0	.12	.86	0	517	160	0	20	176	0	677	196
Witless Bay	0–3	18.2	8.0	5.0	1.5	3.1	0	2076	191	15	174	74	0	2282	248
		(19.4)	(8.0)	(0)	(1.5)	(5.0)	(0)	(2212)	(192)	(0)	(171)	(120)	(0)	(2404)	(291)
Tors Cove	0–3	3.2	6.2	.4	.1	1.3	0	224	312	2	5	13	0	538	18
		(5.3)	(6.2)	(.7)	(.1)	(1.3)	(0)	(370)	(312)	(3)	(4)	(13)	(0)	(685)	(17)
Bauline	0–3	3.0	.8	0	.5	8.6	0	190	4	0	29	43	0	194	72
Brigus South	9–11	.4	2.8	.4	0	3.1	2.7	12	195	3	0	658	76	210	734
		(1.0)	(8.0)	(1.5)	(0)	(9.4)	(9.5)	(30)	(560)	(12)	(0)	(193)	(43)	(602)	(236)
Cape Broyle	13–15	1.6	1.9	.8	.3	1.4	1.2	125	251	31	23	193	43	407	259
		(2.4)	(1.5)	(3.8)	(.4)	(2.3)	(2.0)	(190)	(202)	(138)	(35)	(310)	(74)	(530)	(419)
Calvert	15–20	5.3	9.5	.1	0	1.1	.3	567	712	4	0	79	8	1283	87
		(8.8)	(2.1)	(0)	(0)	(2.0)	(1.0)	(936)	(1612)	(0)	(0)	(130)	(33)	(2548)	(183)
Ferryland	20–25	.1	0	.3	0	.1	0	6	0	7	0	1	0	13	1
Aquaforte	20–25	—	.6	0	—	1.2	0	—	20	0	—	41	0	20	41
			(1.3)	(0)		(2.5)	(0)		(41)	(0)		(83)	(0)	(41)	(83)
Fermeuse	30–50	.4	1.1	1.0	0	.1	0	133	40	20	0	5	0	193	5
		(0)	(.5)		(0)	(0)		(0)	(17)		(0)	(0)		(17)	(0)
Renews	30–50	.9	.2	0	0	0	0	188	5	0	0	0	0	193	0
Portugal Cove	70–80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Totals using															
All reports ($N = 91$)								4052	2123	82	251	889	73	6257	1213
Type 1 reports ($N = 20$) and for Bay Bulls and Bauline, type 2 reports ($N = 13$).								4445	3534	153	259	1662	183	8132	2104

*Bycatch rates and estimated kills calculated from data in Table 5*a*.
†See footnote, Table 4, for colony population statistics.
‡Nets used were cod gill nets (CN), salmon gill nets (SN), and cod traps (CT).
§Numbers in parenthesis are values based on type 1 reports only (most accurate data; see text for details).

number of nets operating in the community fishing area and summing the estimates for the five communities surveyed.

Most murres were caught (N = 906) in cod gill nets (140 mm mesh, nylon monofilament) set at depths ranging from 30 to 100 m; a few birds were also caught (N = 116) in salmon gill nets (nylon, 140–152 mm mesh) set 6–10 m deep. Puffins were rarely caught (N = 11) in cod gill nets, but large numbers were drowned (N = 607) in salmon gill nets. High net-mortalities were recorded near the colonies as well as up to 15 km away and there was a large variation in alcid bycatch from day to day as well as between fishing areas (Table 4). Alcid net-mortality was recorded during similar time periods in all areas surveyed and was correlated with the presence of capelin in each area (as judged by the presence of capelin in cod stomachs).

In summary, it appears that alcids were drowned in fish nets while feeding on capelin and that most murres and puffins were killed in cod and salmon gill nets, respectively. The observed difference in the type of nets responsible for murre and puffin mortality may be due to differences in the feeding behaviour of the two species, with murres feeding at greater depths than puffins. The daily and geographic variation in mortality may be largely due to fluctations in the capelin spawning effort, influenced by oceanographic and meteorological factors (Jangaard 1974).

Taken together, the data indicate that a minimum of 4200 murres and 7900 puffins were killed in gill nets in 1980 in the area sampled. As calculated previously (section 5.2), this represents an adult murre and puffin mortality of 2.7 and 1.6%, respectively, of the local alcid breeding populations. This was the lowest mortality rate of murres observed over the years studied (Table 1). This estimate is probably low as fishing activities were not sampled at all communities (about 14) within foraging distance of the colonies and the overall estimates of fishing gear are known to be conservative. Furthermore, salmon nets were not sampled in two of the five communities surveyed and cod traps were not sampled at all. On the other hand, the estimates of puffin net-mortality may be very high since a large part (85%) of the estimated mortality is derived from the observations of a single fisherman in Cape Broyle (see Table 4).

The year 1980 probably represents a low-point for net-mortality in the Witless Bay Seabird Sanctuary area due to a decline of capelin in inshore waters (J. Carscadden, pers. comm.) and a provincial strike of the Fishermen's Union, which resulted in a major reduction of fishing effort during the 1980 fishing season. This contention is supported by the data (Table 4) which show that there was a marked decline in the time period in which alcid mortality was recorded in Bauline between 1972 and 1980 (17 June – 2 August and 3–10 July, respectively) and, as discussed previously, in the mean number of murres caught per net per season (84.0 and 10.8, respectively).

5.6. Net bycatch survey, 1981

In 1981, a more extensive survey of alcid bycatch around the Witless Bay Seabird Sanctuary was carried out (Tables 1, 5*a*, and 5*b*). The most accurate data were obtained from fishermen recording bycatch and/or from personal observations of bycatch on a daily basis during the capelin spawning period (report type 1, N = 20). The remaining reports (type 2, N = 71) of bycatch were obtained through personal interviews of fishermen before, during, and after the capelin spawning period. Personal observations (J.P.) of seabird bycatch in many communities along the coast (Fig. 1*b*) permitted an evaluation of the reliability of type 2 reports. Coverage of fishing effort in the 17 fishing communities along the coast was extensive (Table 5*a*). Out of an estimated 1560 cod gill nets, 1058 salmon gill nets, and 378 cod traps used from Cape St. Francis to Portugal Cove South (Fig. 1*b*), bycatch was reported (type 1 and 2 reports) from 65, 30, and 30%, respectively, of this gear. Type 1 reports covered 14, 5, and 4% of all fishing gear, respectively, although this coverage was concentrated in areas of high net-mortality from Petty Harbour to Calvert (Table 5*b*).

Considering only type 1 reports, it was observed (Table 6) that most murres (83.3%) were caught in cod gill nets at depths of 30–185 m, whereas relatively few were caught in surface-set salmon gill nets (16.0%) or cod traps (0.7%). In terms of the number of murres caught per net, however, salmon nets were almost as effective in catching murres (8.9 murres/net) as cod gill nets (11.0 murres/net). These data are in rough agreement with the murre band-recovery data discussed previously (Table 3). Almost equal numbers of puffins were caught in salmon (48.0%) and cod (44.7%) gill nets, but in terms of puffins caught per net, more birds were caught in surface-set salmon nets (3.6 puffins/net) and cod traps (1.9 puffins/net) than cod gill nets (0.8 puffins/net). The discrepancy between the rate of bycatch per net and the actual number of birds caught in

Table 6
Comparison of net mortality of Common Murres and Atlantic Puffins in 1981 by type of fishing gear*

Type of fishing gear	No. of nets	Common Murres drowned† No.	%	x̄ no./net	Atlantic Puffins drowned‡ No.	%	x̄ no./net
Cod gill net (138 mm mesh)	220	2423	83.3	11.0	177	44.7	0.8
Salmon gill net (125–138 mm mesh)	52	465	16.0	8.9	190	48.0	3.6
Cod trap (138–200 mm mesh)	15	21	0.7	1.3	29	7.3	1.9
Totals		2909	100		396	100	

*Based on type 1 data only, bycatch recorded daily (see text).
†Maximum depth at which murres were caught = 185 m.
‡Maximum depth at which puffins were caught = 60 m.

Table 7
Summary of the alcid bycatch in the Witless Bay Seabird Sanctuary area in 1981

Report type	No. of reports	No. of birds caught (all nets) Common Murre	Atlantic Puffin
A. Reported bycatch*			
Type 1	20	2909	396
Type 1 and 2	91	4136	635
B. Total bycatch†			
All type 1 and 2	91	6257	1213
Type 1 (8 communities) and selected type 2 (2 communities)	20 13	8132	2104

*Type 1 reports more reliable than type 2 (see text for details).
†Total bycatch extrapolated by calculating x̄ bycatch per net (for each net type) in each community and multiplying this value by the estimated amount of fishing gear in the corresponding community, and then summing for all communities surveyed.

each net type is due to the high ratio of cod gill nets to salmon gill nets and cod traps (4.1:2.8:1, respectively). The fact that more murres were caught in bottom-set cod gill nets than puffins is most likely due to differences in foraging depths between the species.

As in 1972 and 1980, most of the 1981 net-drownings occurred during the inshore spawning migration of capelin (approximately 22 June – 20 July, as judged by the presence of capelin in cod stomachs). Capelin were observed to be the dominant food item (by % occurrence) in murre (97.2%, $N = 71$), puffin (93%, $N = 14$), and cod (48–100%, $N = 259$) stomachs during this period. Most (76%, $N = 1978$) murres in Witless Bay were caught during the first week of the capelin spawning period and the remainder (24%) were caught regularly, but in smaller numbers, for the remainder of time capelin were present. Examination of alcids retrieved from fishing gear revealed that the majority of murres (83.0%, $N = 481$) and puffins (98.4%, $N = 123$) caught were breeding adults (as judged by the presence of well developed brood patches or from autopsies).

The distribution of net-mortality around the Witless Bay Seabird Sanctuary was concentrated within a 60-km zone north and south of the colonies (Table 5*b*). There were few obvious patterns of bycatch observed; rather, there was a great deal of variation in bycatch per net between and within communities. These differences were probably related to capelin distribution, weather conditions, the location of fishing nets, and bathymetric features. If the number of birds caught per net is a valid measure of foraging activity, the data in Table 5*b* suggest that the foraging ranges of murres and puffins are similar (less than 20–30 km) during the capelin spawning period, although small numbers of murres were consistently caught in fishing areas up to 60 km away.

On the basis of reported bycatches, it was possible to extrapolate a total bycatch for the entire southeastern shore fishing area in 1981 (Table 7). Total bycatch was extrapolated (Table 5*a* and 5*b*) as in 1980 and the total amount of fishing gear in use was determined from estimates by fishermen in each community. If all reports ($N = 91$) are considered, about 6300 murres and 1200 puffins were caught in nets in 1981. However, on the basis of observations in the field, it was apparent that some qualitative type 2 reports underestimated actual bycatch. Thus if only the most reliable bycatch reports (all type 1, $N = 20$ and selected type 2, $N = 13$) are used to extrapolate to total bycatch, then about 8100 murres and 2100 puffins were killed in nets in 1981. As before (section 5.2), we calculate that 1981 net-mortality represents an adult murre and puffin mortality equivalent to 3.3–4.2 and 0.25–0.43%, respectively, of the local alcid breeding populations. Murre bycatch was higher than in 1980 (2.7% of breeders), but like 1980, it was substantially less than bycatch observed in the early 1970s (13–20% of breeders). Puffin bycatch in 1981 was markedly lower than in 1980, but, because of extreme intra- and inter-year bycatch variability, it is impossible to evaluate the reliability of the 1980 puffin bycatch estimate. Both the 1972 and 1981 data suggest, however, that puffin net-mortality is usually low relative to murre net-mortality and the 1980 puffin bycatch estimate may therefore be extreme. As discussed previously, the relatively low bycatch rates observed in 1980–81 were probably due to a marked decline in the abundance of capelin spawning stocks inshore (Carscadden, this volume).

5.7. Inshore net-mortality at other seabird colonies

Little is known about alcid net-mortality at the other five major seabird colonies in Newfoundland (Fig. 1*c*) except for anecdotal information which indicates that net-mortality occurs wherever fishing activities coincide with large seabird populations. Capelin are widely distributed around the Newfoundland coast during their spawning migration with major concentrations moving inshore from the southern Labrador – Funk Island Bank region towards the northeast coast (Fig. 1*a*) in June–July (Jangaard 1974) where a large proportion (55%) of gill nets in use in the inshore fishery are located (D. Wells, pers. comm., DFO, Econ. Br., St. John's) in addition to the major seabird populations (Nettleship 1980) at Funk Island (*ca.* 400 000 pairs Common Murres), the Wadham Islands (10 000 pairs Atlantic Puffins), and the Cabot Islands (3000 pairs Common Murres).

Of all Common Murre band recoveries ($N = 334$) over a 26-year period (1951–77) from murres banded as chicks on Funk Island, only 5.8% ($N = 21$) were recovered from fishing gear (CWS files); unfortunately, data are not available to compare bycatch between 10-year periods. Because the murre population on Funk Island has increased dramatically from about 40 000 pairs in 1951 (Tuck 1961) and because there has been an increase in the number of longliner fishing vessels capable of travelling the 60–100 km distance from mainland communities to the Funk Island area (LeMessurier 1980), it is possible that the net-mortality of Funk Island murres is now much greater than the 26-year average band-return figure suggests.

In the Cabot Islands region, net-mortality may also be significant. For example, 340 Common Murres were drowned in six cod gill nets which had been set in the vicinity of South Cabot Island in July 1980 (J. Lien, pers. comm.).

There are no data at present available on alcid net-mortality for the populations (Nettleship 1980) at Baccalieu Island (10 000 pairs of Atlantic Puffin, 1500 pairs of Common Murre) and Cape St. Mary's (11 000 pairs of murre [spp.]). However, personal observations and conversations with local fishermen indicate that net-mortality is common during the inshore capelin spawning period.

A systematic survey of all colony areas is required to evaluate the significance of net-mortality for these other alcid populations.

6. Offshore net-mortality

The potential number of alcids killed in the offshore gill-net fishery is quite high. In 1980, 15 Portuguese gill-netting vessels were licensed to operate within the Canadian 320-km territorial limit from June to December. Of this total, six to 12 boats normally operated (Fig. 1*a*) on the Virgin Rocks (49% of effort), Southeast Shoal (19% of effort), and southwest slope of the Grand Banks (33% of effort), while an equal number of unlicensed vessels operated outside the 320-km limit on the Tail of the Bank and Flemish Cap (D. Kulka, pers. comm., DFO, Econ. Br., St. John's).

This distribution of vessels encompasses all known major alcid wintering grounds in eastern North America. Large numbers of alcids move into these areas between September and December and they remain through to May or June with only small numbers present from July to

September (Brown *et al.* 1975). Thus, there is a 6-month overlap (May–June, September–December) in the use of these biologically productive areas by alcids and commercial gill-net operators. No records of the bycatch associated with these fishing activities are maintained, but qualitative reports from DFO observers (D. Kulka, pers. comm., DFO, Econ. Br., St. John's) and evidence of the bycatch observed during a salmon-tagging exercise conducted by DFO on the Grand Banks in 1979 suggest that it may be high. From 30 April to 20 May 1979, numerous alcids were drowned in salmon gill nets (monofilament nylon, 140–152 mm mesh, 100 m length) placed on the southwest slope of the Grand Banks, Virgin Rocks, Southeast Shoal, and the Tail of the Bank (D. Reddin, unpubl. data). During 384 km-hours of fishing effort, 162 Dovekies, 26 Common Murres, and 2 Atlantic Puffins were recovered from nets set at 6–10 m depths.

The licensed fishing effort of Portuguese gill-netting vessels on the Grand Banks in 1980 for the months of June and September–December is estimated at 132 960 km-h (Table 8). Using the DFO research vessel's ratio of alcids caught per unit fishing effort in May 1980 (Dovekie 0.42, murre 0.068, puffin 0.0052), it is possible that 56 000 Dovekies, 9000 murres, and 700 puffins were killed in offshore gill nets operated within the 320-km limit in 1980. Although the estimates for the kill of murres may be correct, the numbers of Dovekies and puffins drowned are probably much lower than the estimates because cod gill nets are usually set at depths (50–200 m) beyond the normal foraging ranges of these species. However, if a similar net-mortality was associated with the unlicensed gill-netting operations on the Tail of the Bank and Flemish Cap, then the estimated alcid net-mortality would be doubled because the fishing effort in these zones was known to be similar to the effort inside the 320-km limit in 1980.

Table 8
Estimates of gill-net fishing effort by Portuguese vessels on the Grand Banks in 1980*

Month	No. of days on fishing ground (all vessels combined)	Estimate of gill-net fishing effort, km/h†
June	33	15 840
July	124	59 520
August	157	75 360
September	82	39 360
October	74	35 520
November	63	30 240
December	25	12 000
Total	558	267 840

*Does not include fishing effort outside the Canadian 320-km limit which is estimated to be either greater or equal to the fishing effort within Canadian waters (D. Kulka, pers. comm.).
†Calculated by multiplying vessel-days-on-fishing-ground × 24 × number of nets in use per day (x = 200) × total length of nets (0.1 km).

7. Discussion and conclusions

On the basis of murre band recoveries made over 26 years (1951–77) and three surveys of alcid bycatch in fishing nets in the vicinity of the Witless Bay Seabird Sanctuary (1972, 1980, and 1981), as well as numerous qualitative reports, it is apparent that a large bycatch of adult Common Murres and Atlantic Puffins occurs in the area and probably at all other major seabird colonies in Newfoundland. There is some evidence that a substantial alcid bycatch also occurs in offshore fishing regions.

Murre net-mortality appears to have increased dramatically from the 1950s and peaked in the early 1970s as murre populations increased in size and fishing effort intensified in the vicinity of major colonies. In recent years (1977–80), alcid net-mortality has apparently decreased due to a marked decline in the abundance and inshore spawning effort of capelin, the major summer prey item of murres and puffins in Newfoundland.

Meanwhile, there has been a steady increase in effort by the Newfoundland fishery. In 1973 the total number of person-months fished was 59 100 and 55 400 gill nets were in use, whereas in 1979 the numbers of person-months and gill nets were estimated to be 320 000 and 180 400 respectively. During the same period in the fishing zones encompassing the seabird colonies in eastern Newfoundland the number of gill nets in operation increased from 22 500 to 113 500. Thus, there has been a five-fold increase in fishing effort and fishing gear over the last decade. Moreover, traditional fishing grounds are still being exploited and there has been little change in the overall inshore fishing pattern since 1970 (LeMessurier 1980).

It is possible that in past years murre bycatch exceeded the limit allowable for maintaining a stable population, especially for the Witless Bay colonies where band recovery and survey data indicate that 13 to 20% of the breeding population were killed annually in the early 1970s. Even the relatively low murre net-mortality rates observed in 1980–81 (*ca.* 3–4% of breeders) are cause for concern since the total adult murre mortality from all sources (including oil, hunting, and natural mortality) should not exceed 6–12% per annum to maintain stable breeding populations (Birkhead 1974, Mead 1974). Net-mortality of alcids is especially significant because it occurs during the peak of the breeding season and the rearing of young by one bird is difficult, if not impossible (Nettleship 1972).

If capelin stocks recover, it is reasonable to expect that a high alcid bycatch will be seen in coming years, particularly in view of the increased emphasis on and participation in the inshore fishery in Newfoundland. Indeed, preliminary analysis of the 1982 capelin spawning effort in Newfoundland suggests that it was much larger than in recent years (J. Carscadden, pers. comm.). Correspondingly, murre bycatch in fishing nets increased two- to three-fold in the Witless Bay area, and increased bycatch was noted at other seabird colonies as well.

Clearly, more research is required to elucidate the impact of net-mortality on seabirds in Newfoundland, as well as a concerted effort to better understand the population biology of the seabirds most vulnerable and their major summer prey, capelin, a fish species that forms the basis of the food web in temperate water regions of Atlantic Canada (Brown and Nettleship, this volume).

8. Acknowledgements

This research was funded by the CWS with supplemental support for J. Piatt by a Newfoundland Provincial Government Special Scholarship for Resource-Related Studies and Memorial University of Newfoundland. This study is part of the program "Studies on northern seabirds," Seabird Research Unit, CWS, Environment Canada (Report No. 114). We thank R.G.B. Brown and A.J. Erskine for reviewing the manuscript and providing useful suggestions.

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Recent trends in the west Greenland salmon fishery, and implications for Thick-billed Murres

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1. Abstract

In the late 1960s and early 1970s, a high net-mortality of seabirds, particularly Thick-billed Murres (*Uria lomvia*), was associated with the west Greenland salmon fishery. Since 1972, the domestic fishery has been controlled by quotas and fishery opening dates and the non-Greenlandic offshore drift-net fishery was phased out in 1975. These restrictions probably resulted in a substantial decrease in murre net-mortality. However, the Greenlandic fishery has changed considerably since 1972 when seabird bycatch was last examined in detail. Fishing vessels now use monofilament nylon nets almost exclusively; fishing effort has redistributed closer to murre breeding colonies and intensive drift-netting occurs offshore on the continental shelf. These factors, combined with a change in 1981 to a later fishing season, have probably resulted in a renewal of significant murre net-mortality at west Greenland.

2. Résumé

Vers la fin des années 1960 et au début des années 1970, le taux élevé de mortalité d'oiseaux aquatiques dans des filets de pêche, en particulier de Marmettes de Brünnich (*Uria lomvia*) a été associé à la pêche au saumon à l'ouest du Groenland. Depuis 1972, la pêche locale est réglementée par la fixation de contingents et de dates d'ouverture tandis que la pêche hauturière nongroenlandaise aux filets dérivants a été abolie en 1975. Ces restrictions ont probablement entraîné une baisse considérable du taux de mortalité des marmettes dans les filets. Toutefois, la pêche groenlandaise a changé considérablement depuis 1972, année à laquelle les dernières captures d'oiseaux aquatiques ont été analysées en profondeur. Aujourd'hui, les navires de pêche utilisent presque exclusivement des filets en nylon monofilament; l'effort de pêche s'est redistribué près des colonies de marmettes nicheuses, et une pêche intensive aux filets dérivants a pris naissance au large, sur le plateau continental. Ces facteurs, associés au recul de la saison de pêche en 1981, ont probablement fait renaître les taux de mortalité élevés de marmettes dans les filets à l'ouest du Groenland.

3. Introduction

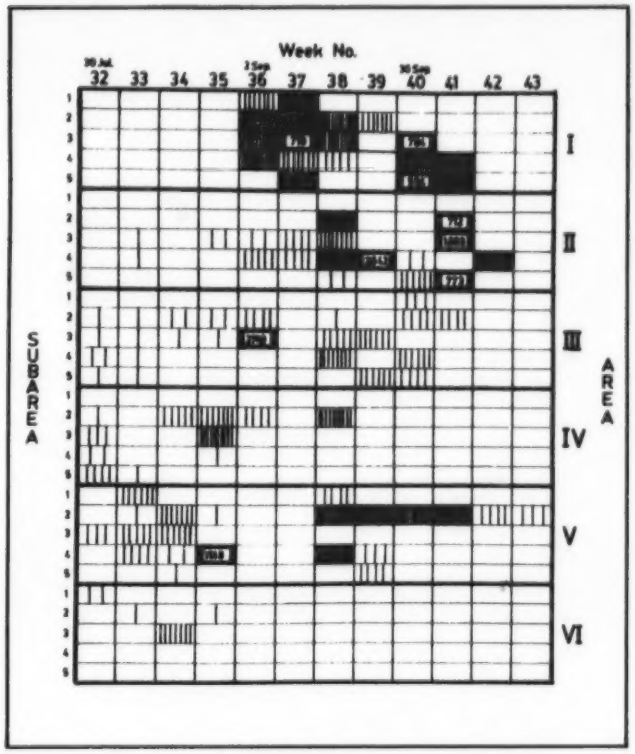
Each fall, millions of Thick-billed Murres (*Uria lomvia*) from Greenland and the eastern Canadian Arctic migrate south along the west coast of Greenland (Gaston 1980). During migration, large concentrations of these murres feed underwater on small fish, especially capelin (*Mallotus villosus*) which form dense post-spawning schools on offshore banks (Salomonsen 1967, Jangaard 1974). Migrating Atlantic salmon (*Salmo salar*) also feed intensively on capelin at west Greenland (Lear 1980) and an offshore drift-net salmon fishery has existed there since the 1960s (Reddin and Burfitt 1980). International attention was focused on west Greenland in the late 1960s and early 1970s when domestic and especially foreign fishing activity resulted in excessive salmon catches (Anon. 1980, Kreiberg 1980) and a large incidental bycatch of seabirds, particularly Thick-billed Murres (Tull *et al.* 1972, Christensen and Lear 1977). In 1976, Evans and Waterston suggested that the combined bird mortality from net-drowning, hunting, oil pollution, and colony disturbance exceeded annual recruitment for those Thick-billed Murre populations. This concern was supported by colony censuses which showed that both Greenlandic (Evans and Waterston 1976) and Canadian (Nettleship 1977) Thick-billed Murre populations had significantly declined over the previous 20 years.

4. Murre net-mortality: the 1970s

In order to evaluate recent murre bycatch in the west Greenland fishery with respect to the location and duration of fishing effort, we re-interpreted (Fig. 1) the data of Christensen and Lear (1977). They quantified murre bycatch (number of murres caught per 100 mile-hours of salmon drift-net fishing effort) on a weekly basis (from 30 July – 21 October) in 30 discrete zones (6 north/south areas and 5 east/west subareas) along the west coast of Greenland (Fig. 2). It is clear from the data (Fig. 1) that most murre bycatch in drift-nets occurred as murres staged on the Disko banks and the banks off Holsteinborg from early September (64%) to mid October (22%). While bycatch (43%) occurred in offshore zones (12–60 nautical miles [nm]), most bycatch (57%) occurred in neritic waters less than 12 nm from the coast. The extreme variability of murre bycatch is obvious (Fig. 1) and the cause of these fluctuations (e.g. weather, sea-state, etc.) are discussed by Christensen and Lear (1977). Periods of exceptionally high murre bycatch per fishing effort (Fig. 1) probably resulted from the combined concentration of murre and salmon feeding activity on capelin.

The total salmon catch and fishing effort in west Greenland waters has decreased since 1973 in accordance with the International Commission for the Northwest Atlantic Fisheries (ICNAF) recommendations of 1972 (Reddin and Burfitt 1980). The domestic Greenland fleet has maintained a quota since 1973, usually caught by early September, of 1190 t per year up to 1980. The foreign offshore

Figure 1
Murres caught in salmon drift nets at west Greenland, 1972, per 100 mile-hours of nets. Each vertical line represents 20 murres caught; maximum number per block is 20 lines or 400 murres. Blocks containing numbers with black borders represent exceptionally high murre bycatch and the number displayed is the actual bycatch for that week (not prorated). Blank blocks result from zero fishing effort, not absence of bycatch. Adapted from Christensen and Lear (1977)



drift-net fishery, which took about 850 t annually, was phased out completely by 31 December 1975 (Reddin and Burfitt 1980). Regulation of the salmon fishery by a quota and opening date set by the Danish government (Anonymous 1980) has led to increasingly earlier fishing seasons from 1975 (20 August – 12 September) to 1979 (1–28 August). This effectively shifted fishing effort away from the time period during which birds were most likely to be caught in nets (Fig. 1) and during which a greater fishing effort was required to catch salmon (Christensen and Lear 1977).

Based on this time shift of fishing effort, reduced offshore fishing activity, and the data of Christensen and Lear (1977), we calculated that, from 1976–80, murre bycatch in salmon nets was reduced to about 10–20% of that calculated by Tull *et al.* (1972) for 1969–71 (500 000 ± 50%) or Christensen and Lear (1977) for 1972 (207 000 by non-Greenlandic vessels). However, changes in the operation and type of fishing gear used by Greenlandic fleets (Table 1) and the imposition of later fishery opening dates beginning in 1981, may have resulted in a renewal of significant murre net-mortality at west Greenland.

5. The recent domestic Greenland salmon fishery

In 1972, Greenlandic drift-net vessels were usually small, fished close to shore during daylight hours, and used a higher proportion of more visible multifilament nylon

Table 1
Comparison of the domestic West Greenland salmon fishery in 1972 and 1981

1972	1981
Mostly stationary multifilament gill nets set in fiords and near shore.	Almost exclusively monofilament drift nets, set inshore and off shore.
Mostly small "open boat" fishing vessels.	Many mid-size longliners and some large ocean-going fishing vessels.
Drift nets fished in daylight hours only.	Drift nets fished day and night.
Fishing effort widely distributed along coast.	Fishing effort concentrated on northern banks.

nets than did the non-Greenlandic fleet (Christensen and Lear 1977). In recent years (1976–80), the majority of the salmon quota (959 t in 1980) has been taken in larger vessels which venture farther off shore, with the balance of the quota (231 t) taken in small boats near shore.

At present, the standard fishing gear (Kreiberg 1980) is a light-coloured monofilament nylon gill net (130–140 mm mesh, 38 m in length). Mainly fished as drift-nets, a fleet is composed of many (up to 100) of these nets joined together (typically 2–3 km). Although these nets are checked in daylight (Kreiberg 1980), they are usually left in the water overnight, and poor weather may result in gear being unattended for several days and nights (Kreiberg 1980). These are important factors since Christensen and Lear (1977) found that 97% of murre net-entrapment occurred in nets set overnight.

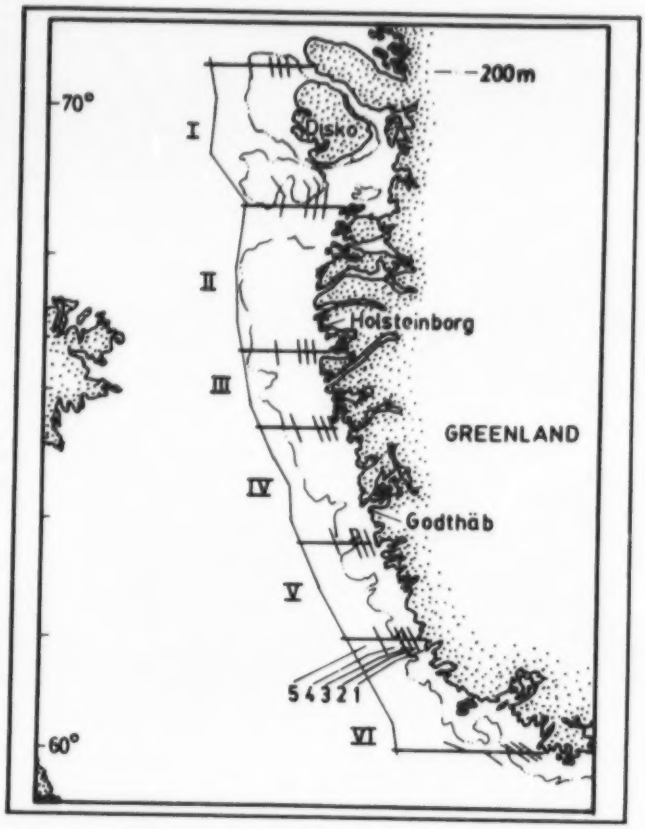
The distribution of salmon fishing effort has shifted considerably from the early 1970s when most (67% in 1973, Anon. 1980) salmon were taken south of Godthaab to the late 1970s when most (71% in 1979, Anon. 1980) salmon were taken north of Godthaab. This is significant in terms of murre mortality since Christensen and Lear (1977) found that, in 1972, 84% of all murre net-mortality occurred north of Godthaab (Figs. 1 and 2).

In 1981, the fishery was opened on 25 August. The large vessel quota was caught by 10 September and the small boat quota was reached sometime in mid October. Of all the changes in the domestic Greenland fishery discussed above, the timing of the quota is probably the most significant in terms of murre net-mortality.

6. Conclusions

Recent net-mortality studies have shown (Piatt *et al.* this volume, Ainley *et al.* 1981) that the bycatch of seabirds in fishing gear is highly variable and depends on many factors including the abundance and distribution of prey, mesh size and type of nets involved, fish and seabird migration patterns, and the proximity of fishing effort to colony sites. Because the Greenlandic salmon fishery now utilizes monofilament nylon nets, nets are usually left in the water overnight, fishing effort has redistributed to more northerly locations, intensive drift-netting occurs within a 25-km distance from the coast, and the recent trend is to open the salmon fishery later in the year; we predict that there has been an increase in Thick-billed Murre and other seabird net-mortality at west Greenland. In view of the fact that Greenlandic and eastern Canadian arctic Thick-billed

Figure 2
Area map of west Greenland showing fishing areas I–VI and subareas 1–5. Subareas (1–5) extend over whole coastline but are segmented here for clarity. The subareas are defined as: 1, inside the baseline; 2, baseline – 6 nm; 3, 6–12 nm; 4, 12–30 nm; 5, 30–60 nm. Adapted from Christensen and Lear (1977)



Murre populations have already suffered substantial reductions in numbers (Nettleship 1977), a re-investigation of net-mortality at west Greenland should proceed in the future to establish whether the salmon fishery is once again significantly affecting arctic murre populations.

7. Acknowledgements

This work was supported in part by a Newfoundland Government "Special Scholarship for Resource-Related Research" and the Canadian Wildlife Service (CWS), Environment Canada. The authors are grateful to J. Gibson, H. Lear, D.N. Nettleship, J. Pippy, R. Porter, and W. Threlfall for critically reviewing the manuscript. This investigation is associated with the program "Studies on northern seabirds," Seabird Research Unit, CWS, Dartmouth, N.S. (Report No. 128).

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Marbled Murrelet mortality due to gill-net fishing in Barkley Sound, British Columbia

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1. Abstract

Alcid mortality due to nearshore commercial fishing has been seldom examined. Little information is available on how it occurs and what effects it has on local populations. During studies of a breeding population of Marbled Murrelets (*Brachyramphus marmoratus*) in 1979 and 1980, in Barkley Sound, British Columbia, we obtained information on mainly Marbled Murrelet mortality due to a local, sockeye salmon (*Oncorhynchus nerka*) based, gill-net fishery. The fishing season coincided with the murrelets' nestling period and regular high-density aggregrations of fishing boats and feeding murrelets overlapped. Most mortality occurred at night in the southern part of Trevor Channel. This mortality is significant because 7.8% of the fall population size is killed annually. Mortality has probably happened only recently, however, due to changes in fishing boundaries. Mortality could be effectively eliminated by excluding gill-net fishing from a small area where foraging Marbled Murrelets aggregate or by allowing "daylight" fishing only in this area.

2. Résumé

La mortalité des alcidés due à la pêche commerciale près des côtes a rarement été étudiée. On dispose de peu d'informations sur la façon dont elle survient et sur ses répercussions sur les populations locales. Au cours d'études réalisées sur une population nicheuse d'Alques marbrées (*Brachyramphus marmoratus*) en 1979 et en 1980, à Barkley Sound en Colombie Britannique, les auteurs ont recueilli des données sur la mortalité des alques résultant principalement de la pêche locale du saumon sockeye (*Oncorhynchus nerka*) au filet. La saison de pêche coïncidait avec la période de nidification des alques et régulièrement, de grandes quantités de bateaux de pêche venaient empiéter sur le territoire où se nourrissent ces espèces. La plupart des décès survenaient la nuit dans la partie sud du canal Trevor. Ce taux de mortalité est appréciable, car 7,8 % de la population d'automne est tuée chaque année. Toutefois, ces cas sont probablement récents, et seraient dus aux modifications des limites des zones de pêche. La mortalité dans les filets pourraient être éliminée en interdisant la pêche aux filets dans les petites zones où des groupes d'Alques marbrées viennent s'alimenter ou en n'autorisant dans cette région que la pêche pendant le jour.

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3. Introduction

Much concern has recently developed over the adverse effects that commercial fishing activities have on marine bird communities (Straty and Haight 1979). Considerable attention has been directed towards the incidental mortality of seabirds in offshore salmon gill-net fisheries (King *et al.* 1979, Ainley *et al.* 1981). Off Greenland, large numbers of murres (*Uria* spp.) were netted over several years (Tull *et al.* 1972, Christensen and Lear 1974). This mortality seemed to exceed the reproductive capacity of the breeding population and led to the closure of the fishery in some areas (Salomonsen 1979). Gill-net fishing in nearshore waters appeared to kill fewer seabirds and to be less significant. Large tolls, however, have been inflicted near large nesting colonies (King *et al.* 1979; Piatt *et al.*, this volume).

In this paper, we report the mortality of alcids, primarily Marbled Murrelets (*Brachyramphus marmoratus*), from a nearshore gill-net fishery in Barkley Sound, Vancouver Island, British Columbia. By examining dead alcids and the abundance and distribution of alcids and of gill-net boats, we discover factors that cause murrelets to become tangled in gill nets. We can then estimate the impact of gill-net mortality on the Barkley Sound breeding population. This localized mortality points to differences between nearshore and offshore net mortality. These differences need to be considered when determining the significance of this mortality.

4. Methods

Alcid mortality was determined during a study of Marbled Murrelet foraging ecology that was conducted from May through September (1979) and June to October (1980) in Barkley Sound, British Columbia (Fig. 1). All dead alcids, found floating or received from a Fisheries and Oceans Canada patrol boat, were salvaged. In 1980, a request for birds incidentally killed by commercial trolling, purse-seining, and gill-net fishing was posted on 7 June at three fish-delivery and packing plants in Bamfield. Fishery workers were asked to record, for each bird captured, the date, location, time of day, type of fishing gear used, and depth of capture, if known. Supplementary information on numbers and species of birds killed was obtained through casual discussions with fishermen and fishery officers. All specimens were deposited in the University of Manitoba Zoology Museum.

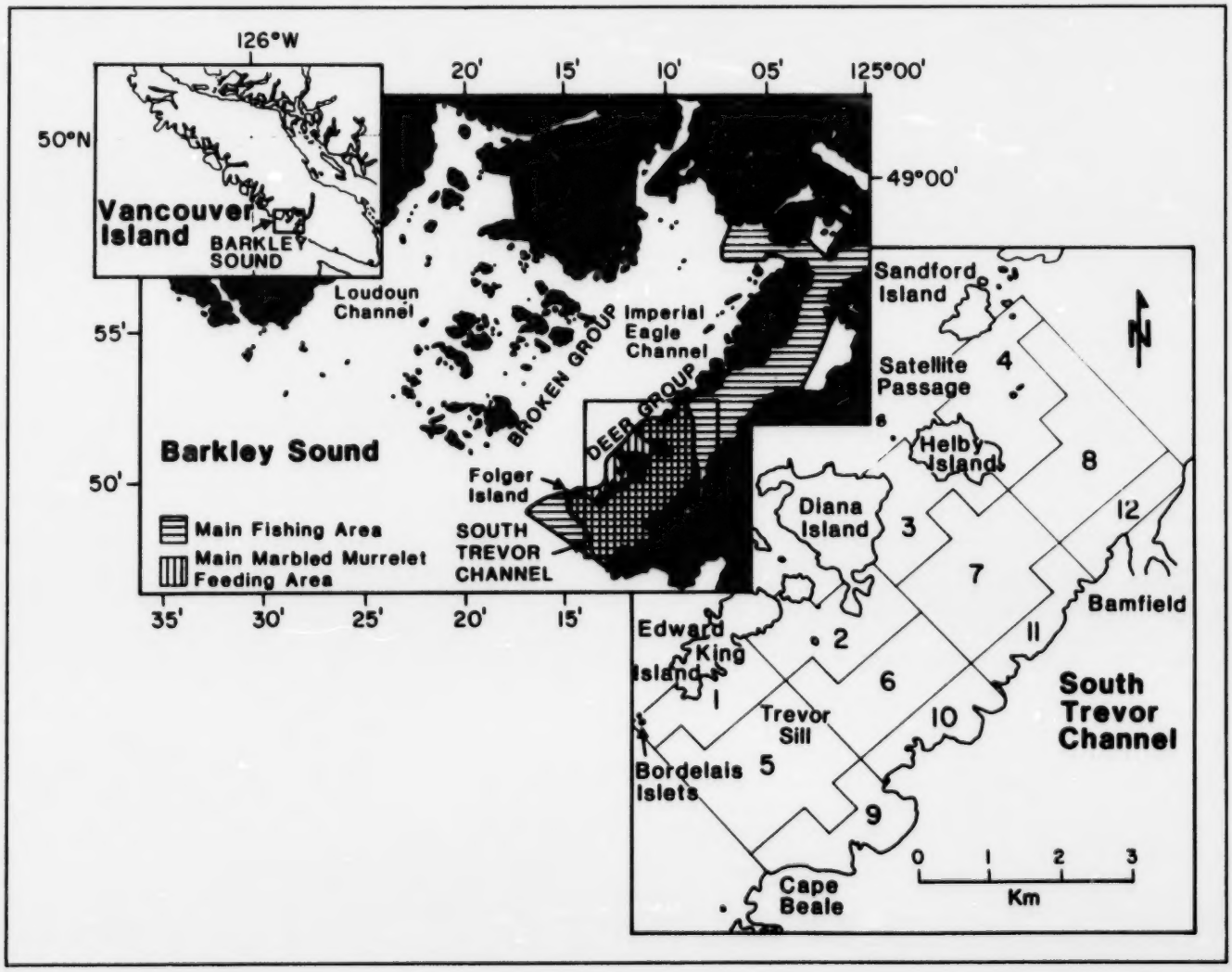
The abundance and distribution of alcids and gill-net boats were examined where aggregations of each overlapped in Trevor Channel (Fig. 1). In 1980, 37 censuses of alcids and boats were conducted on a 24-km^2 grid (later separated into 12 subareas) which we refer to as South Trevor Channel (Fig. 1). Censuses were made at four times of day (05:00, "dawn"; 10:00, "morning"; 15:00, "afternoon"; and 20:00, "dusk") and each census took 2–2.5 h. Censuses were conducted from a pneumatic boat with one observer between 16 June and 6 July. The numbers of all alcids were recorded but flying birds were not included in the calculation of bird densities. Gill-net boats were censused in 18 of the 37 censuses, during fishery openings. Boats were noted as "fishing" (if nets were set or being manipulated) or "not fishing." Visibility was adequate to record total numbers of boats for two adjacent areas in South Trevor Channel in 15 of 18 boat censuses.

5. Results

5.1. Aspects of alcid gill-net mortality in Barkley Sound

Forty-four alcid carcasses were obtained during the fishing season in the two summers (12 in 1979 and 32 in 1980). Twenty-four carcasses were provided by five fishermen (1980), nine were received from a fisheries patrol boat, and 11 were found dead on the water. Thirty-three birds had been killed in gill nets. Six floating carcasses were fresh, had torn neck feathers and salmon scales on feathers, and resembled birds known to have been killed in gill nets. Five other floating carcasses were excluded because they were somewhat decomposed and appeared to have died from other causes. All birds were obtained between 11 June and 17 July. Birds were killed in multifilament nylon nets that were 135–375 m in length, less than 10 m in depth, with

Figure 1
Locations in Barkley Sound, British Columbia, that were used by fishing boats and Marbled Murrelets; and the location of South Trevor Channel where boats and murrelets were censused in numbered subareas



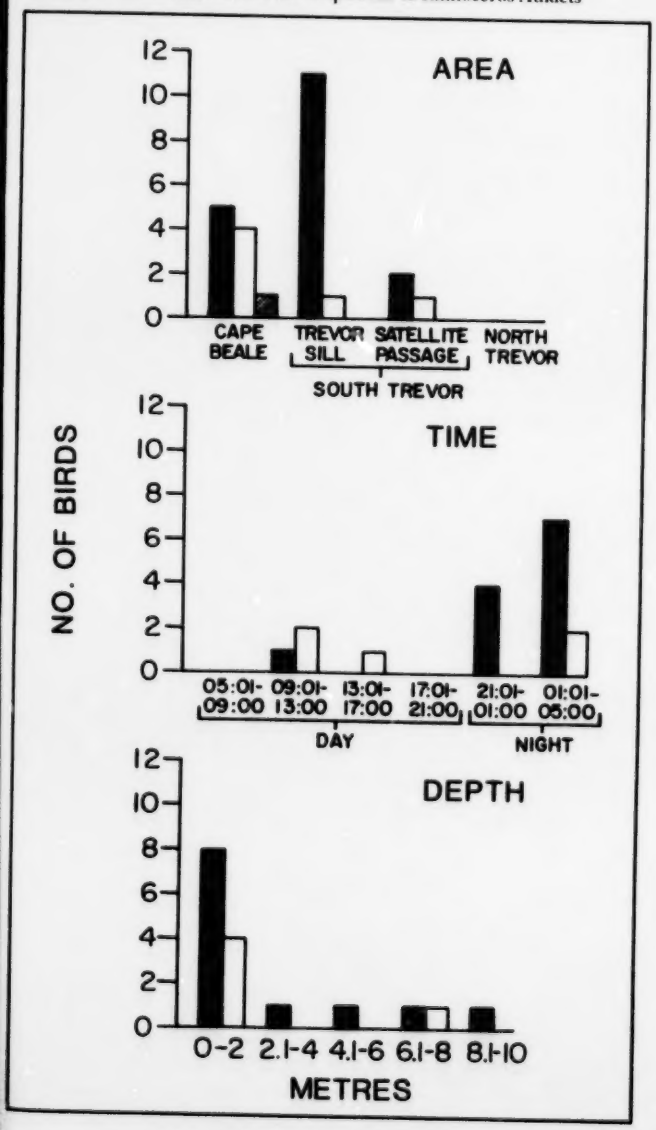
mesh sizes of 10–13 cm (see Pacific Commercial Salmon Fishery Regulations and BC Fishery (General) Regulations made under the 1978 Fisheries Act for other gill-net specifications).

The Marbled Murrelet was the most frequently killed alcid ($n = 28$), but Common Murres (*Uria aalge*) ($n = 10$) and Rhinoceros Auklets (*Cerorhinca monocerata*) ($n = 1$) were also killed. Most (93%) Marbled Murrelets were breeding (based on the presence of a brood patch) but one non-breeding and one hatching-year (HY) bird were also killed. One non-breeding Rhinoceros Auklet, and four breeding and six non-breeding Common Murres were killed. There were no obvious differences in the numbers of each sex in the sample of birds obtained.

Most birds were killed off Cape Beale and the Trevor Channel sill area, at the southern end of South Trevor Channel (Figs. 1, 2). More Marbled Murrelets were killed in the sill area, whereas more Common Murres were killed off Cape Beale. Marbled Murrelets were killed almost exclusively at night; however, Common Murres were killed at night and during the day (Fig. 2). Most birds were killed within 2 m of the surface. A few were taken deeper, at a maximum of 8.5 m (Fig. 2).

As only a few fishermen provided birds, these data may be biased with regard to fishing time and location. However, the patterns were confirmed through casual discussions with fishermen, including fishermen who found birds dead in their nests but did not keep them. Many fishermen did not provide dead birds because they were suspicious or did not want to make labels.

Figure 2
Aspects of alcid gill-net mortality in Barkley Sound. Cape Beale and North Trevor areas are shown in Figure 6 and Trevor Sill and Satellite Passage areas are shown in Figure 1. Dark bars refer to Marbled Murrelets, open bars to Common Murres, and the striped bar to Rhinoceros Auklets



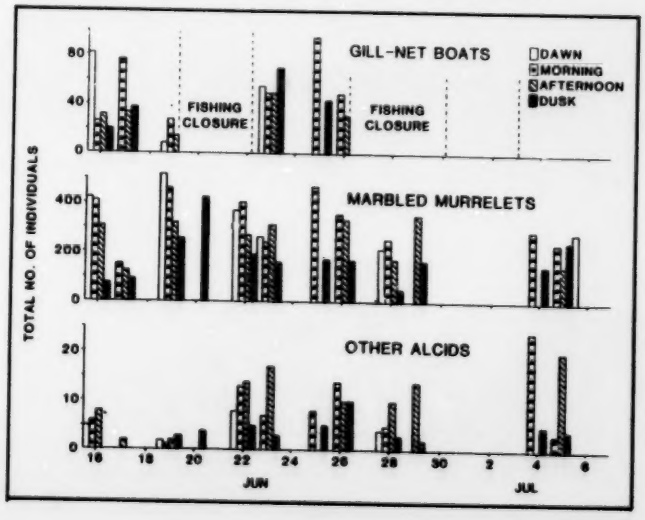
5.2. Alcid abundance and distribution in South Trevor Channel

During the count period, the Marbled Murrelet was the most abundant alcid in South Trevor Channel and averaged 265.8 ± 118.3 birds/census (Fig. 3). Pigeon Guillemots (*Cepphus columba*), Common Murres, and Rhinoceros Auklets averaged 4.6 ± 5.8, 1.5 ± 2.2, and 0.5 ± 0.9 birds/census, respectively. Therefore, murrelets were found in the highest mean densities (11.26 ± 4.95 birds/km^2) followed by Pigeon Guillemots (0.19 ± 0.25), Common Murres (0.06 ± 0.10), and Rhinoceros Auklets (0.02 ± 0.04).

Marbled Murrelets were unevenly distributed in South Trevor Channel: densities were higher in subareas along the shores, particularly of the Deer Group islands, and lower in mid channel except in subarea 5, which had moderate densities (Fig. 4). Very few murrelets occurred north of the count area in Trevor Channel at this time (Carter and Sealy, pers. obs.). Pigeon Guillemots were also unevenly distributed and found in subareas along the shore, while Common Murres and Rhinoceros Auklets were found more randomly but in the seaward half of South Trevor Channel (Fig. 4).

On average, Marbled Murrelets were more abundant during dawn and morning censuses (14.4 and 13.9

Figure 3
Total numbers of gill-net boats, Marbled Murrelets and three other alcid species for each census ($n = 37$) in South Trevor Channel. (Notes: Marbled Murrelets were seen on each of the 37 censuses whereas gill-net boats and other alcids were not; no other alcids were recorded on 16 June (dusk), 17 June [morning and dusk], 23 June [dawn], and 6 July [dawn])



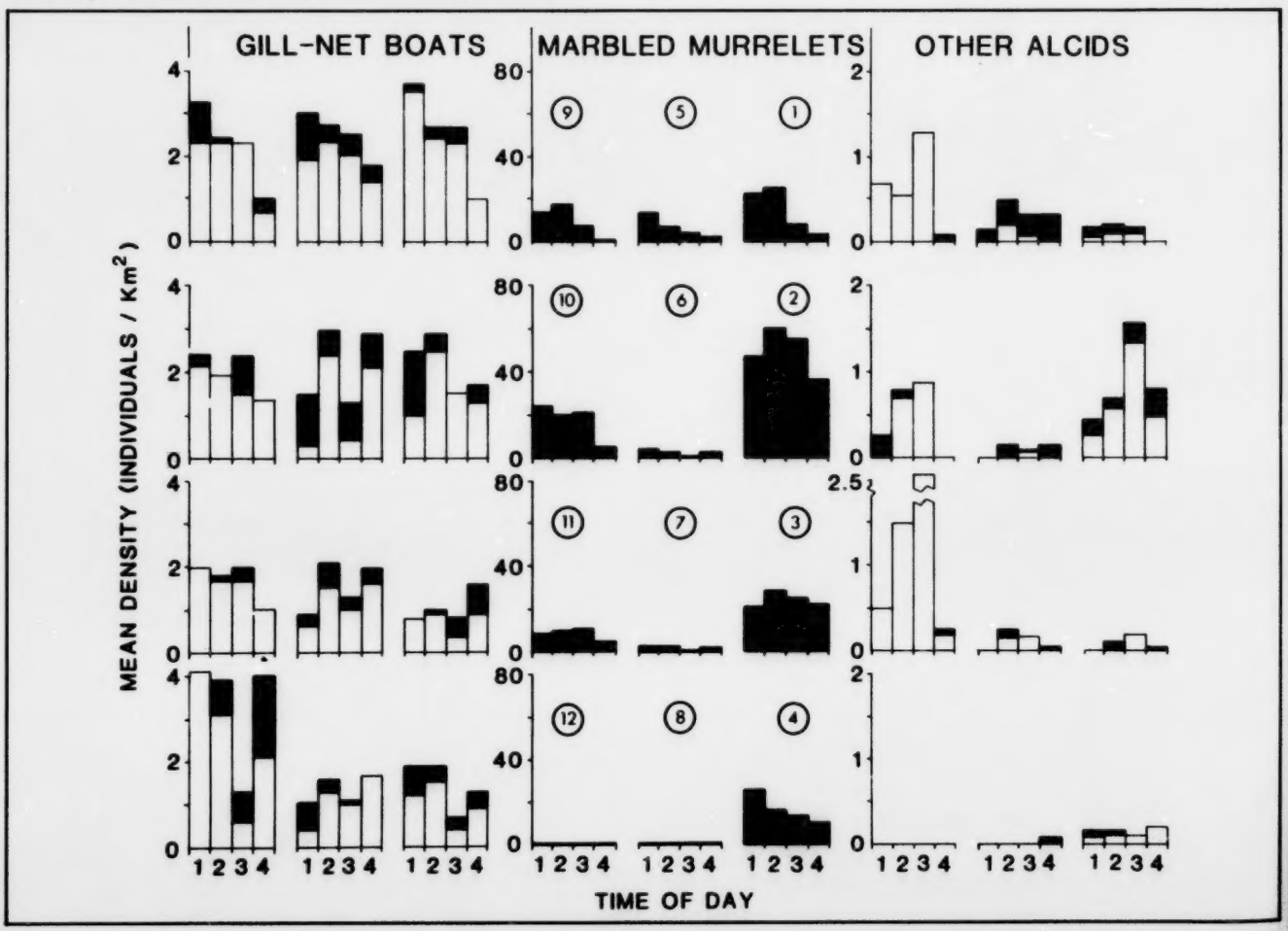
birds/km^2, respectively) becoming less abundant in afternoon (11.0 birds/km^2) and dusk (7.7 birds/km^2). Murrelets were clumped throughout the day particularly in subareas 2 and 3 (Fig. 4). Smaller numbers remained in all areas throughout the day. Pigeon Guillemots were more abundant during morning and afternoon censuses (0.24 and 0.39 birds/km^2, respectively) and were clumped in subareas 2, 9, 10, and 11 at these times. Common Murres and Rhinoceros Auklets were too uncommon to identify any diurnal patterns (Fig. 4).

Marbled Murrelets regularly formed large gatherings in South Trevor Channel from late May to early August in 1979 and 1980, presumably in response to a localized food resource (Carter and Sealy 1980). The nesting location of these murrelets, however, was not determined. They probably nest solitarily along heavily forested coasts and adjacent inland areas of Barkley Sound (Sealy and Carter, in press). Non-breeding murrelets also occur in the aggregation (borne out by collecting; also see Sealy 1974, 1975). A few small colonies of other alcids near South Trevor Channel are probable sources of breeding birds observed during counts. Seabird Rocks supports 150 nesting pairs of Rhinoceros Auklets and 50 pairs of Pigeon Guillemots; a few scattered pairs of Pigeon Guillemots also nest in the Deer and Broken Group islands (Guiguet 1971, Hatler *et al.* 1978). The nearest Common Murre colony is at Tatoosh Island, Washington, where 100 pairs nest (Wahl *et al.* 1981). Based on the number of birds present at sea, the Marbled Murrelet is the most abundant breeding seabird in Barkley Sound (Guiguet 1971; Hatler *et al.* 1978; Sealy and Carter, in press).

5.3. The gill-net fishing season in Barkley Sound

The fishing season in Barkley Sound (statistical area 23 defined in Pacific Commercial Salmon Fishery Regulations; see map in British Columbia Commercial Fishing Guide [1981:79]) is presently regulated through four phases: (1) February to May; (2) early June; (3) late June to late July; and (4) short openings in fall (Fig. 5). Gill-net fishing is permitted in phase 1, but little fishing occurs due to mesh-size restrictions. Starting in phase 2, an influx of boats occurs (in 1979, 62 gill-net boats were present at opening). By phase 3, the peak influx of boats occurs (in

Figure 4
Mean densities of gill-net boats, Marbled Murrelets, and three other alcid species in each subarea (shown in Figure 1) in South Trevor Channel (indicated by circled numbers) and for each time of day (coded as 1, dawn; 2, morning; 3, afternoon; and 4, dusk). Gill-net boat bars indicate mean densities of boats fishing (open) and not fishing (dark). Other alcid bars represent Pigeon Guillemots (open), and Common Murres and Rhinoceros Auklets (dark)



1979, 215 gill-net boats; 1975–79, 207 boats average). At the end of phase 3, gill-net fishing is shifted into Alberni Inlet, to control the harvest of salmon from specific spawning rivers. Barkley Sound proper is closed to gill-net fishing from late July to February, except for occasional short openings that may occur in phase 4.

5.4. Abundance and distribution of gill-net boats in South Trevor Channel

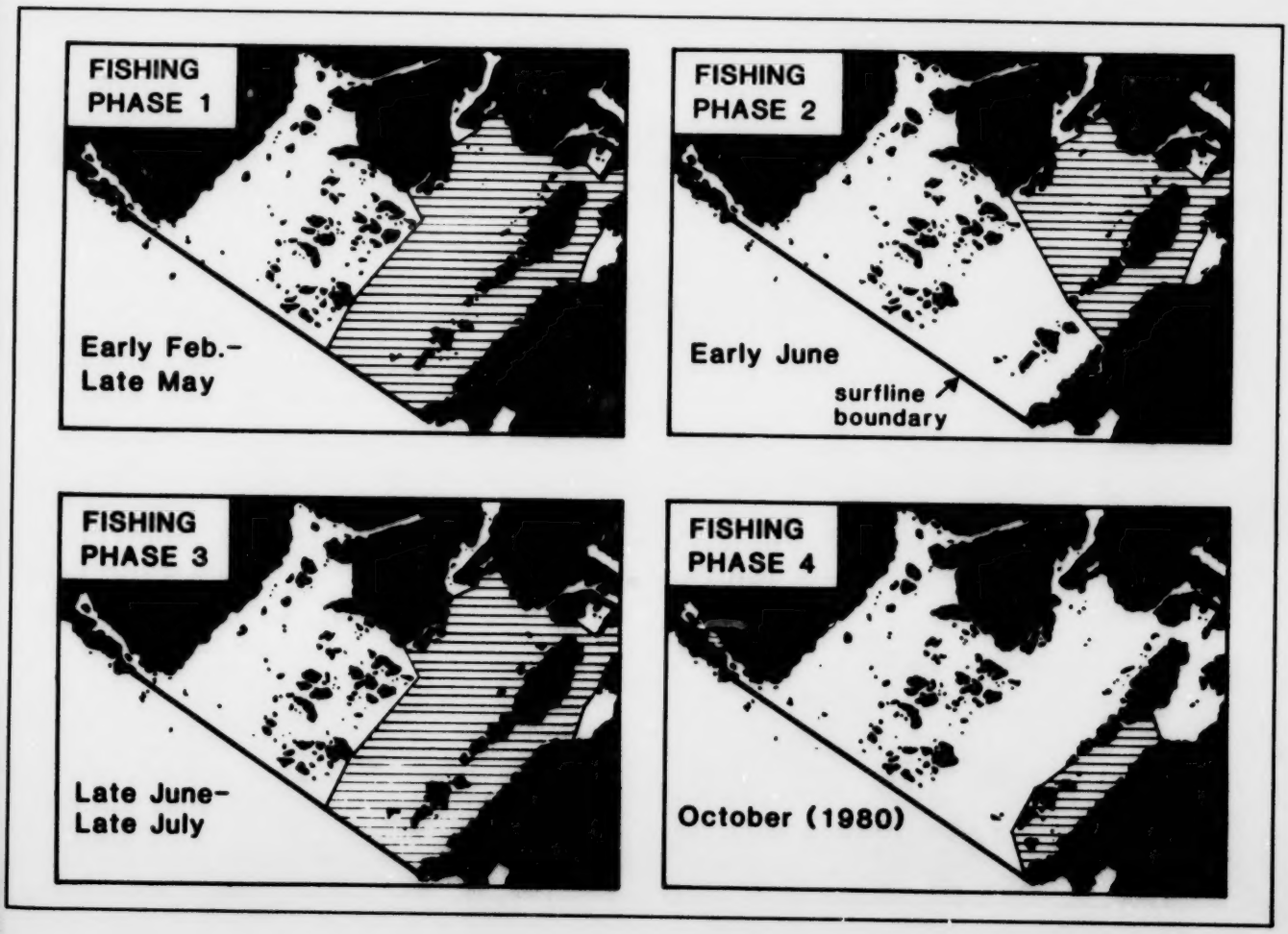
Gill-net boats were censused during phase 3 of the fishing season: South Trevor Channel contained an average of 44.4 ± 23.8 boats/census; the Cape Beale and North Trevor Channel areas contained only 28.1 ± 15.1 and 15.3 ± 19.9 boats/census, respectively (Fig. 6). Densities of gill-net boats averaged 2.00 ± 1.00 boats/km^2, in South Trevor Channel. Densities could not be calculated for the two adjacent areas because the area censused was not measured. Boats may have been in higher densities off Cape Beale than in South Trevor Channel for this area is smaller (Fig. 6).

Gill-net boats were almost evenly distributed in South Trevor Channel although, on average, more boats were found near the sill (subareas 1, 5, 9) (Fig. 4). The highest mean density, however, occurred in subarea 12, adjacent to Bamfield Inlet (2.71 ± 1.88 boats/km^2). Densities of boats "fishing" averaged 1.57 ± 0.88 boats/km^2.

In South Trevor Channel, mean numbers of boats were fairly consistent between times of day, whereas at Cape Beale, numbers were higher in the morning (39.8 boats/census) and at North Trevor, higher at dusk (29.8 boats/census) (Fig. 6). With all three areas combined, mean numbers were highest in morning (103.7 boats/census) and lowest in the afternoon (56.8 boats/census). Within South Trevor Channel, the highest mean densities (2.27 boats/km^2 occurred in the morning (when 84% of the boats were fishing) and the lowest mean densities (1.60 boats/km^2) in the afternoon (when 78% of the boats were fishing). At dawn and dusk, 69% and 76% of the boats were fishing, respectively.

During phase 3, gill-net boats tended to fish in Trevor Channel (particularly South Trevor Channel). Most

Figure 5
Gill-net fishing boundaries by phase in Barkley Sound in 1979–80. Areas open to fishing are striped



of Imperial Eagle Channel, which was open to fishing, was not used. Regulations restricted fishing to usually 3–4 days and nights a week and this probably accounted for the regular presence of large numbers of boats throughout the permitted days. Gill-net boats were small (about 10 m in length) and each boat set out one net in a straight line (often perpendicular to shore) for varying periods of time. This allowed for high densities of boats. Boats were spaced apart to prevent interference and were thus evenly distributed in South Trevor Channel. Generally, fishermen delivered fish once a day and often moved to Bamfield to dock, if they were not fishing at night. These movements accounted for the number of boats not fishing during counts. Fewer boats fished at night, judging by the number of lights that were visible from Bamfield.

6. Discussion

6.1. Tangling of Marbled Murrelets in gill nets

Alcids are highly susceptible to being killed in gill nets because they dive to obtain food (Ainley *et al.* 1981). The number of birds that are killed is related to the number, density, and variability of nets and birds where they co-occur. However, the relationship between bird-net encounters, and birds diving and becoming tangled in nets is obscure and may involve feeding and/or escape behaviour.

6.1.1. *Co-occurrence of murrelets and gill nets* — Large mean numbers of Marbled Murrelets and gill-net boats were present in Barkley Sound during phase 3 of the fishing season (Fig. 7). The clumped dispersion patterns of murrelets and boats promoted murrelet mortality where high-density aggregations overlapped in South Trevor Channel. Other alcids which occurred in lower densities were caught less often. If fishing occurred later in the summer or more intensively in phase 4 (Fig. 5), fewer birds would have been killed because murrelets were distributed in small and widely scattered flocks while moulting (Fig. 7).

Murrelets were present in high densities throughout the day (and probably at night) whereas gill-net boats were present in high densities only during openings. The alternation of closings and openings may have reduced the numbers of birds killed but probably intensified fishing effort, and thus boat densities, during each opening.

6.1.2. *Attraction of murrelets to gill nets* — Murrelets were often observed in small flocks landing near or sitting beside nets during the day. Birds may have been attracted to nets to feed on small schooling fish that collected at the net interface (e.g. herring [*Clupea* spp.], Parrish 1969). Birds were observed "surface seizing" and diving, probably to obtain fish near nets. M. E. "Pete" Isleib (*in litt.*) also believed that the presence of small fish attracted Marbled Murrelets to nets in Prince William Sound, Alaska. He recorded murrelets "usually in singles or pairs swimming along nets and diving, often surfacing on one side and then the other." Birds may recognize nets by the styrofoam floats that line their tops (Melville 1973). Most murrelets, however, were not observed near nets in the day. Birds may have been opportunistic and attracted to nets from a short distance or some avoidance may have occurred. Thus, during the day, fewer murrelets may have encountered nets than might be expected at random from observed densities.

6.1.3. *Night mortality and murrelet distribution* — All murrelets that were killed in gill nets at night (Fig. 2) were breeding. Based on brood-patch scores (Sealy 1974), birds were either incubating or feeding nestlings. A few birds had food in their stomachs, indicating that at least some birds were feeding themselves at night. As most murrelets were killed near the top of nets, birds may have been foraging near the surface. Isleib (*in litt.*) also noted that murrelets were caught within 3–5 m of the surface. Simons (1980) suggested, however, that murrelets may make many nocturnal,

Figure 6
Mean numbers of gill-net boats by area and time of day

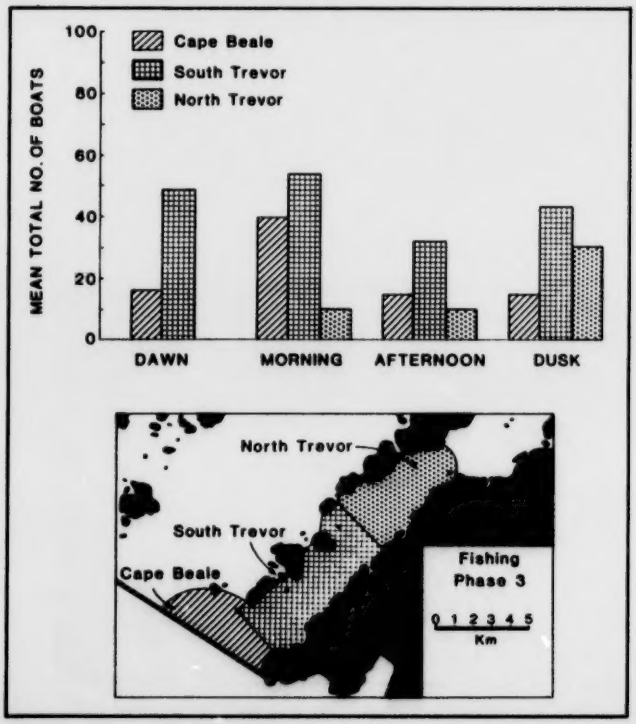
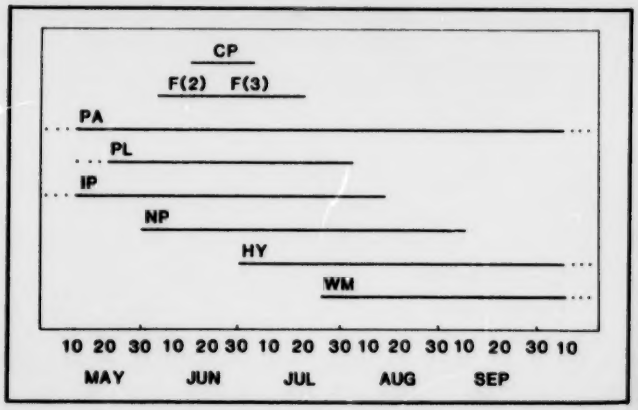


Figure 7
Breeding phenology of the Marbled Murrelet in relation to the gill-net fishing season in Barkley Sound, 1979–80. Phenology designations, in part, follow Sealy (1974): CP, census period; F, fishing season phase; PA, presence of adults, PL, presence of large numbers of murrelets in South Trevor Channel; IP, incubation period; NP, nestling period; HY, fledged young at sea; WM, wing moult period; and , . . . , extremes unknown



nestling-feeding trips. Thus, some birds (that were killed with empty stomachs) may have been foraging for their young. Night foraging by Marbled Murrelets has been previously suggested by observations of birds flying inland throughout the night (Carter and Sealy, unpubl. data) and is supported by birds being killed throughout the night in South Trevor Channel (Fig. 2). Bailey (1977) also suspected that murrelets were feeding at night near the Kenai Peninsula, Alaska, and Isleib (*in litt.*) indicated that most (>80%) murrelets were killed at night in Prince William Sound, Alaska. Christensen and Lear (1974) demonstrated that murres were also killed mainly at night off Greenland and suggested that individuals were better able to "evade" nets during the day. Nylon nets may have been less visible to murrelets at night (Bibby 1973), as has been shown for some fish (Hamley 1975). This may account for more bird kills at night, although foraging occurs during the day and night.

Marbled Murrelets in South Trevor Channel may have different distribution patterns at night, which further increased their susceptibility to becoming tangled. In subareas, 1, 5, 9, and 10, a dramatic increase in mean numbers occurred between dusk and dawn censuses (Fig. 4). Most mortality was reported from this area (Trevor Sill); yet these areas did not have the largest daytime murrelet densities. More murrelets, more gill-net boats, and/or more foraging may have occurred there at night. Thus, the frequency of bird-net encounters and numbers of birds killed may have been greater. If true, this factor would greatly reduce the value of daytime counts of abundance and distribution. Similarly, McMahan and Fritz (1967) noted that Redheads (*Aythya americana*) were distributed differently at night, depending on weather, and on certain nights were more susceptible to being hooked on trotlines. Breeding Pigeon Guillemots, in South Trevor Channel, may have reduced their susceptibility at night by staying at the nest site; large numbers were observed only on morning and afternoon censuses (Fig. 4) and none were obtained or reported killed.

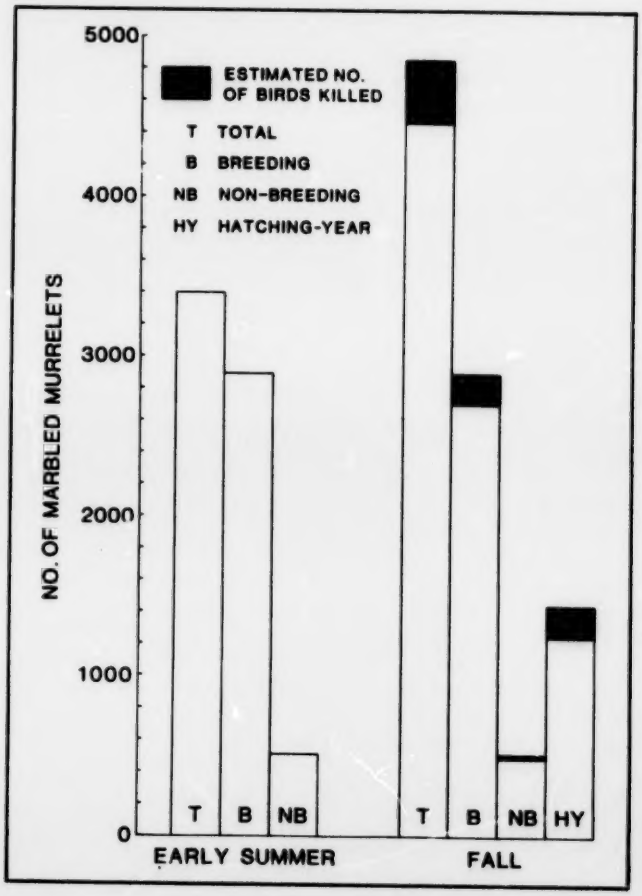
6.2. Impact of gill-net mortality on the local Marbled Murrelet population

The dispersed solitary nests of Marbled Murrelets could make the species less susceptible to gill-net mortality (King *et al.* 1979). However, the aggregative behaviour of murrelets at sea during the nesting period makes them susceptible where aggregations co-occur with gill-net fishing areas. Since specific murrelet nesting areas are not known, it is not possible to directly determine whether numbers of nesting individuals are declining due to gill-net mortality. Thus, to determine the impact of gill-net mortality on Marbled Murrelets in Barkley Sound requires some speculation.

It was difficult to estimate how many murrelets were killed annually in Barkley Sound from the small sample of dead birds obtained. Since 17 murrelets were obtained from five fishermen in 1980 and on average about 70 gill-net boats were present in areas where most birds were killed, possibly as many as 250 murrelets were killed. Fishermen that were interviewed also indicated that they caught "some" (or "many") murrelets each season, including in 1980. However, most birds were killed at night when less fishing occurred. We believe that between 175 and 250 murrelets were killed in 1980.

In Barkley Sound, there are an estimated 3400 murrelets (Sealy and Carter, in press). About 15% of the birds were probably non-breeding (Sealy 1974). Therefore, the breeding population consisted of 2890 birds or 1445 pairs. By extrapolating from the sample of dead birds obtained, we estimated that breeding, non-breeding, and HY individuals constituted 90%, 5%, and 5% of the total number of murrelets killed in gill nets, respectively. Using a conservative estimate of 200 birds killed in gill nets/year, 180 breeding, 10 non-breeding and 10 HY birds were therefore killed. By adding 180 nestlings that did not fledge (because 180 breeding birds were killed in gill nets), to the number of HY birds killed in gill nets, we determined the total impact on the population of HY birds in the fall (Fig. 8). We estimated that a total of 380 murrelets were killed in 1980, of which 47%, 3%, and 50% were breeding, non-breeding and HY birds, respectively (Fig. 8). Thus, an estimated 6.2% of the breeding individuals were killed. Additionally, 13.1% of potential young were not raised to fledging (assuming one nest attempt per year, one parent cannot raise the young, and both members of the pair were not killed), or were killed in nets. Also, 2% of the non-breeding birds were estimated to have been killed. If no gill-net mortality had occurred and excluding natural mortality, the fall population size would have been 4845 birds. With gill-net mortality, the fall population size was estimated to be 4465 birds. Thus, 7.8% of the potential fall population died in gill nets in 1980.

Figure 8
Estimated impact of gill-net mortality on Marbled Murrelet numbers in Barkley Sound in 1980



The possible long-term effects of mortality caused by nearshore fishing have not been widely recognized. Because the numbers of birds found killed are generally low (often in the low hundreds [Bibby 1971, 1973; Melville 1973]), nearshore mortality has not been considered to be as significant as larger offshore mortality (King *et al.* 1979). Since nearshore mortality is probably sustained annually on the same population, the cumulative effect could be great. Cobb (1976) has demonstrated that the continuous toll inflicted on murres by nearshore fishing was important and vastly outweighed numbers killed by oil spillage near St. Andrew's Bay, England. Murrelet (and other inshore seabird) populations are sensitive to additional unnatural mortality caused by gill-net fishing because of their lower numbers compared to offshore feeding seabirds (Diamond 1978, Sowls *et al.* 1980, Wahl *et al.* 1981). Whether reductions occur in Barkley Sound will depend on murrelet immigration, emigration, and recruitment; the permanence of South Trevor Channel as the main feeding area for murrelets; and, the persistance of high-density gill-net fishing, over the long term.

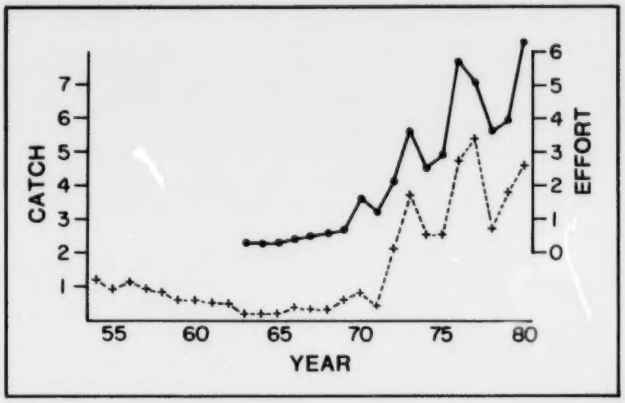
6.3. Gill-net fishing trends

The movement of the fishing boundary out to "surfline" in phase 3 (Fig. 5) has produced the overlap of gill-net boats and feeding murrelets in South Trevor Channel and near Cape Beale. However, fishing has only been allowed out to the "surfline" since 1978. Earlier, the phase 2 boundary remained in effect until the late summer closure of the Barkley Sound fishery. The fishing season has also been shortened since 1978. In 1975–77, gill-net fishing started in mid May and ended in late August (Salmon Expectations and Proposed Fishing Patterns 1975–1980). Within each season from 1975 to 1980, openings were 4 days per week but, in 1980, they were reduced to 3 days per week. Also, phase 2 was reduced to one opening in 1980.

In relation to these regulation changes, fishing effort was lower in 1978 and 1979. In 1980, however, the largest annual gill-net fishing effort (number of days fishing) occurred (Fig. 9). Since openings were shorter in 1980 (and the length of the fishing season was much the same as in 1979), probably more gill-net boats fished in South Trevor Channel in 1980 than in previous years. However, because gill-net fishing only began in that area in 1978 and bird mortality was only measured in a year when fishing effort was high, the estimated kill of Marbled Murrelets in 1980 probably reflects a higher than average mortality than elsewhere in the Barkley Sound fishing area.

The size of fishing catches in future years will largely determine the persistance of high-density gill-net fishing in Barkley Sound. The fishery is presently based on sockeye salmon (*Oncorhynchus nerka*) stocks which have been successfully enhanced (Robinson and Barraclough 1978). How long these stocks can withstand the steadily increasing fishing pressure (Fig. 9) is not known. However, Barkley Sound has an early and annually consistent fishery that has attracted many boats from other fishing areas. Long-term gill-net fishing in Barkley Sound can be expected, as can long-term gill-net mortality of murrelets.

Figure 9
Salmon catch and gill-net fishing effort (1954–80) in Barkley Sound. The broken line refers to catch (total number of salmon caught, in thousands) and the solid line to effort (total number of days fishing, in thousands). Data from BC Catch Stat. Dep. Fish. Oceans Canada. Pac. Reg. Vancouver.



6.4. Conservation measures

We believe that the mortality of Marbled Murrelets in gill nets in Barkley Sound is significant and suggest that it be further examined. This nearshore mortality could have immediate consequences because it is directed on a small population and occurs annually. At present, the geographic extent of the gill-net mortality of murrelets is not known, although it occurs in Prince William Sound, Alaska, and is suspected to occur throughout southeastern Alaska (Isleib, *in litt.*). It has also been recorded in Monterey Bay, California, in winter (D. Croll, *in litt.*). Susceptible populations of Marbled Murrelets may be identified by censuses at sea and monitored regularly over the long term to detect changes (see Sealy and Carter, in press).

In Barkley Sound, two measures would reduce the mortality of murrelets in gill nets. First, if salmon catches were unaffected, the exclusion of gill-net fishing (perhaps by maintaining the phase 2 fishing boundary (Fig. 5) during phase 3) in South Trevor Channel and off Cape Beale only, would eliminate the overlap of aggregations of murrelets and gill-net boats (Fig. 1). A similar measure has been considered in Monterey Bay, California, where a rapid growth in the gill-net fishery has caused a drastic increase in nearshore seabird mortality (Heneman 1981). Also, Bartonek (1965) suggested that certain areas of Lake Winnipegosis, Manitoba, could be closed to commercial fishing if reductions of Redheads continued to occur. Second, gill-net fishing could be prohibited at night, when most murrelet mortality occurs. Daylight fishing could be extended through longer openings and salmon catches probably would not be affected. This measure has been previously enforced in other fishing areas in British Columbia, although not for conservation reasons (S. A. Benoit, pers. comm.).

7. Acknowledgements

Our field work on murrelets was funded by Canadian Wildlife Service scholarships to Carter and grants from the Natural Sciences and Engineering Research Council of Canada (G0232 and G0753) to Sealy. We thank R.E. Foreman and J.E. McInerney for their support and for

making available to us the facilities of the Bamfield Marine Station. We also thank the Bamfield fishing community and Fisheries and Oceans Canada fishery officers for their co-operation. S.A. Benoit and K. Lorette of the Operations Unit, Fisheries and Oceans Canada (Pacific Region, Vancouver) provided salmon catch and effort statistics, public notices, salmon expectations and proposed fishing patterns, commercial fishing guides, fishery regulations, and fishery officer reports. M.E. "Pete" Isleib provided useful information on the gill-net mortality of murrelets in Alaska. S.A. Barton, J.D. Carter, J.M. Porter, and J. Rosenberg assisted in the field and E. Chew provided computer advice. S.A. Benoit provided helpful comments on gill-net fishing trends. The reviews by W.B. King, D.A. Manuwal, and I. Robertson have greatly improved the manuscript.

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